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NEW SPECIES AND ADDITIONAL RECORDS OF THE TACHYINE *PHILIPIS* ERWIN
(COLEOPTERA: CARABIDAE: BEMBIDIINAE)

MARTIN BAEHR

Baehr, M. 2002 5 31: New species and additional records of the tachyine *Philipis* Erwin (Coleoptera: Carabidae: Bembidiinae). *Memoirs of the Queensland Museum* 48(1): 1-7. Brisbane. ISSN 0079-8835.

As a supplement to the Revision of the genus *Philipis* Erwin (Baehr 1995) three new species are described: *P. unistriata* sp. nov. from Mt Elliot near Townsville, *P. striatoides* sp. nov. from Mt. Murray Prior near Cairns, both northern Queensland, and *P. inexpectata* sp. nov. from Gibraltar Range in northern New South Wales. The latter is the first record of the genus from outside of Queensland. Additional records of 20 known species are recorded, slightly enlarging the geographic or altitudinal range in some cases. □ *Coleoptera, Carabidae, Philipis, Queensland, new species.*

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As a supplement to the revision of the tachyine *Philipis* Erwin (Baehr, 1995) additional records of described species are presented that have been since collected by G. B. Monteith and co-workers of the Queensland Museum on mountains of eastern Queensland, some being mountain tops that had not been worked before. Some records enlarge the geographical range or the altitudinal range of certain species, and of some species that were known from few specimens only, additional material now is at hand. This may justify recording of all localities. Also three new species are described. One is of special interest, because it represents the first record of any *Philipis* in northern New South Wales.

A few species have been collected by members of the Cooperative Research Centre for Tropical Rainforest Ecology and Management, Cairns. Such records are marked CRC, those from Queensland Museum are without special labelling.

Species are arranged in alphabetical order. Format of the descriptions follows that used in Baehr (1995).

***Philipis alticola* Baehr**

Baehr, 1995: 324.

ADDITIONAL RECORD. 1 ex, NEQ: 17°24'S, 145°45'E, Bartle Frere, S. Peak summit, 29 Nov 1998, G. Monteith, Pyrethrum trees/logs, 1620m, 1977.

NOTE. This species was known from a single specimen collected at the summit of Bellenden Ker; its range is extended to include the top of adjacent Mt. Bartle Frere.

***Philipis alutacea* Baehr**

Baehr, 1995: 354.

ADDITIONAL RECORDS. 1 ex, Bellenden Ker Range, NQ, Summit TV Stn., 1560m, 17 Oct.-Nov. 5, 1981, EARTHWATCH/QLD. MUSEUM Pyrethrum knockdown; 3 ex, NEQ: 17°24'S, 145°45'E, Bartle Frere, S. Peak summit, 29 Nov 1998, G. Monteith, Pyrethrum trees/logs, 1620m, 1977.

NOTE. This species was known from Bellenden Ker only; its range is extended to the summit of adjacent Mt. Bartle Frere.

***Philipis bicolor* Baehr**

Baehr, 1995: 361.

ADDITIONAL RECORDS. 22 ex, NEQ: 16°30'S 145°19'E, Mt. Demi summit, 1000m, 16-17 Dec 1995, Monteith, Pyrethrum, trees.

NOTE. The new record is from within the known range.

***Philipis castanea* Baehr**

Baehr, 1995: 331.

ADDITIONAL RECORD. 1 ex, NEQ: 16.11S 145.24E, Pimm's Block (Grove), 1000m, FIT PO6F, 13 Mar-8 May 1998, S. Grove, 8097 (CRC).

NOTE. The new record is from just south of the known range.

***Philipis cooki* Baehr**

Baehr, 1995: 325.

ADDITIONAL RECORD. 1 ex, NEQ: 16°31'S 146°16'E, Mt Lewis Rd (Hut) 14 July 1996, 1200m, G. B. Monteith, Pyrethrum, trees.

NOTE. The new record is from within the known range.

***Philipis distinguenda* Baehr**

Baehr, 1995: 366.

ADDITIONAL RECORD. 1 ex, NEQ: 16°30'S 145°16'E, Hilltop, 18 km N Mt Lewis 23 Nov 1998, G. B. Monteith. Pyrethrum trees. 1300m. RF. **1939**.

NOTE. The new record slightly enlarges the range of this species to the south.

***Philipis frerei* Baehr**

Baehr, 1995: 351.

ADDITIONAL RECORDS. 11 ex, NEQ: 17°24'S 145°45'E, Bartle Frere, S. Peak summit, 29 Nov 1998, G. Monteith, Pyrethrum trees/logs, 1620m, 1977.

NOTE. The new record is from within the known range.

***Philipis laevigata* Baehr**

Baehr, 1995: 326.

ADDITIONAL RECORDS. 2 ex, NEQ: 16°26'S 145°12'E, Mt. Spurgeon Summit, 21 Nov 1997. 1320 m, G. B. Monteith **1637**, Pyrethrum, trees & logs (QMB).

NOTE. The new record is from within the known range.

***Philipis lustrans* Baehr**

Baehr, 1995: 367.

ADDITIONAL RECORDS. 7 ex, NEQ: 16°56'S 145°51'E, Mt Murray Prior, 7 Dec 1995, G. Monteith, Pyrethrum, trees & logs; 4 ex, NEQ: 16°56'S 145°51'E, Mt. Murray Prior, 31 Oct 1995, 770m, Monteith & Cook, Pyrethrum, trees & rocks; 8 ex, NEQ: 16°56'S 145°51'E, Mt. Murray Prior, 7 Dec 1998, G. Monteith, Pyrethrum, trees. *Casuarina* **2034**.

NOTE. The new records are from within the known range.

***Philipis picta* Baehr**

Baehr, 1995: 359.

ADDITIONAL RECORDS. 1 ex, NEQ: 15°47'S 145°19'E, Mt. Hartley summit 8 Nov 1995-16 Jan 1996, Monteith, Cook & Roberts, Pitfall traps, 790 m; 1 ex, NEQ: 15°47'S 145°19'E, Mt. Hartley. 750 m. 8 Nov 1995. G. Monteith Pyrethrum, trees & logs.

NOTE. The new record slightly enlarges the range of this species to the south. Sampling in pitfall traps is rather unusual for species of genus *Philipis*, because they generally live on tree trunks.

***Philipis planicola* Baehr**

Baehr, 1995: 341.

ADDITIONAL RECORDS. 8 ex, NEQ: 17°17'S 145°58'E, Graham Range, 550m, 1 Nov 1995, G. Monteith, Pyrethrum, trees & logs; 2 ex, NEQ: 17°17'S 145°58'E, Graham Range, 550m, 8-9 Dec 1995, Monteith, Thompson & Cook, Pyrethrum, trees & logs.

NOTE. The new records are close to the recorded range, but the altitude range is greater than reported before, because the species was recorded previously only in lowland. Nevertheless, this does not really seem to be a montane species.

***Philipis rufescens* Baehr**

Baehr, 1995: 355.

ADDITIONAL RECORDS. 2 ex, Bellenden Ker Range, NQ, Summit TV Stn., 1560m, 17 Oct.-Nov. 5, 1981, EARTHWATCH/QLD.MUSEUM Pyrethrum knockdown; 3 ex, NEQ: 17°16'S 145°51'E, Bellenden Ker, 1994 Crash site. 1 Dec 1998, G. Monteith. Pyrethrum trees. 1325m **1992**.

NOTE. The new record is from within the known range.

***Philipis ruficollis* Baehr**

Baehr, 1995: 334.

ADDITIONAL RECORD. 1 ex, NEQ: 15°49'S 145°17'E, Mt. Finnigan summit, RF, 1100 m, 20-22 Nov 1998, G. Monteith, P. Bouchard & A. O'Toole. **1928**.

NOTE. The new record is from within the known range.

***Philipis sinuata* Baehr**

Baehr, 1995: 365.

ADDITIONAL RECORDS. 2 ex, Bellenden Ker Range, NQ, Summit TV Stn., 1560m, 17 Oct.-Nov. 5, 1981, EARTHWATCH/QLD. MUSEUM Pyrethrum knockdown; 1 ex, AUST: QLD: NE: Bellenden Ker, summit TV stn. 16 Apr 1999, G. B. & S. R. Monteith/QM berlesate 993, 17°16'S 145°51'E, Rainforest, 1500 m, Moss ex trees & logs; 1 ex, NEQ: 17°54'S 145°41'E, Mt Kooroomool, summit 7 km S, 3 Dec 1998, Monteith, 1050m, Dungtrap, 7.30-10.00 pm. NIGHT, **2009**; 30 ex, NEQ: 17°24'S 145°45'E, Bartle Frere, S. Peak summit, 29 Nov 1998, G. Monteith, Pyrethrum trees/logs, 1620m, **1977**; 9 ex, NEQ: 17°24'S 145°49'E, Bartle Frere, Top Camp, 1500m, 29 Nov 1998, G. Monteith, Pyrethrum trees, R.F. **1978**.

NOTE. The new records are from within the known range.

***Philipis striata* Baehr**

Baehr, 1995: 339.

ADDITIONAL RECORDS. 1 ex, NEQ: 16.13S 145.24E, Hutchinson Ck (Grove) 30 m, FIT HO3F, 11 Feb-14 Mar 1998, S. Grove 2900 (CRC); 1 ex, NEQ: 16.09S 145.24E, Cooper Creek (Grove) 140 m, FIT CO1F, 10 Feb-16 Mar 1998, S. Grove 2722 (CRC).

NOTE. The new records are from localities just outside the known range.

***Philipis subtropica* Baehr**

Baehr, 1995: 353.

ADDITIONAL RECORDS. 2 ex, QLD: SE: Mt. Bithongabel, Lamington Nt. Pk. 8 Oct 1979, G. B. Monteith/ QM Berleseate Nr. 203 Rainforest stick brushing; 1 ex, SEQ: Mt. Bithongabel, Lamington NP, 8 Oct 1979, G. Monteith Pyrethrum on *Nothofagus*.

NOTE. The new records are from within the known range.

***Philipis sulcata* Baehr**

Baehr, 1995: 350.

ADDITIONAL RECORDS. 10 ex, NEQ: 16°30'S 145°16'E, Hilltop, 18 km N Mt Lewis 23 Nov 1998, G. B. Monteith. Pyrethrum trees, 1300m. RF. 1939.

NOTE. The new record enlarges the range of this species slightly to the south.

***Philipis thompsoni* Baehr**

Baehr, 1995: 346.

ADDITIONAL RECORDS. 3 ex, AUST: QLD: NE: Upper Boulder Ck. 8 km N. Tully, 7 Dec 1989 Monteith Thompson Janetski/ Q.M. Berleseate No. 828, 145.55°E. 17.50°S. Rainforest, 1000m, Moss; 2 ex, NEQ: 16°55'S 145°40'E, Mt. Williams, 0.5 km NW, 28 Nov. 1997. 870m, G. B. Monteith. 1662, Pyrethrum, trees & logs; 3 ex, NEQ: 17°13'S 145°25'E, 3 km W. Bones Knob, 10 Dec 1995, 1100m, Monteith Cook Thompson, Pyrethrum, trees & logs; 2 ex, NEQ: 17°26'S 145°42'E, Hughes Rd. Topaz, 650m, 4 Dec 1993, Monteith & Janetzki, Pyrethrum, trees & logs; 1 ex, NEQ: 17°36'S 145°42'E, Maalan Rd. 2 km S. of Palmerston Hwy, 750m, 18 May 1995, G. Monteith, Pyrethrum, tree bases; 5 ex, NEQ: 17°54'S 145°41', Mt Kooroomool, summit 7 km S, 4 Dec 1998, 1050m, G. B. Monteith, Pyrethrum trees & logs, 2011; 3 ex, NEQ: 17°54'S 145°41', Mt Kooroomool, saddle 7 km S, 3 Dec 1998, G. Monteith, Pyrethrum trees, 860m, 2006; 12 ex, NEQ: 17°33'S 145°33'E, Mt Fisher, summit, 1360 m, 8 Feb 1999, rainforest, GB Monteith, pyrethrum trees & logs, 2176; 1 ex, NEQ: 17°33'S 145°33'E, Mt Fisher, ½ km NW, 8 Feb 1999, 1280 km R/F. GB Monteith, pyrethrum trees & logs, 2178; 3 ex, 17°36.945S 145°47.748E, Palmerston Nt. Pk. QLD, Pyrethrum mist, Planted Trans. 1, 30 m, 2 Dec 2000, C. Ozanne (CRC).

NOTE. The new records of this very widespread fully winged species are within the known range.

***Philipis tribulationis* Baehr**

Baehr, 1995: 345.

ADDITIONAL RECORDS. 1 ex, Windsor Tableland, N.Qld. 27 Dec 88 - 9 Jan 1989, E. Schmidt & ANZSES Site 3, flt. intercept; 1 ex, AUST: NQ: 16°23'S 145°17'E, Upper Whyanbeel Ck. 5 Sept 1992. 1150 m, G. Monteith. Pyrethrum, mossy rocks.

NOTE. The new records are from within the known range.

***Philipis unicolor* Baehr**

Baehr, 1995: 332.

ADDITIONAL RECORD. 1 ex, Bellenden Ker Range, NQ, Cable Tower 3, 1054m, 17 Oct.-Nov. 5.1981, EARTHWATCH/QLD.MUSEUM Pyrethrum knockdown.

NOTE. The new record is from within the known range.

***Philipis unistriata* sp. nov.**
(Figs 1, 2A)

ETYMOLOGY. Refers to the absence of all striae except for the sutural stria.

MATERIAL EXAMINED. HOLOTYPE: ♂, AUST: QLD: NE: Mt Elliot, NE slope, 5 Dec 1986, G. Monteith G. Thompson/ Q.M. Berleseate No.724, 19.29°S 146.48°E. Rainforest 1000m, Litter (QMT 93348).

DIAGNOSIS. Medium sized, rather convex species, with s-shaped fascia in posterior half of elytra. Distinguished from all species with similar elytral pattern (except *P. tribulationis*) by presence of the sutural stria only. From the latter species easily distinguished by distinctly wider pronotum and 4-setose parameres.

DESCRIPTION. *Measurements*. Length: 2.15mm; width: 1.05mm. Ratios: Width pronotum/head: 1.54; width/length of pronotum: 1.67; width base/apex of pronotum: 1.40; width widest diameter/base of pronotum: 1.08; length/width of elytra: 1.29.

Colour: Dark piceous, base to anterior 1/3 or 1/2 and apex of elytra slightly lighter, posterior half of suture even lighter, reddish-piceous. Elytra with a well-defined, contrasting, oblique, s-shaped, light reddish fascia in posterior 2/5 medially reaching 2nd stria. Legs yellow.

Head. Median antennomeres c. 1.3 x as long as wide. Microreticulation distinct on labrum and anterior border of clypeus, superficial and rather difficult to see on frons, absent on vertex, about isodiametric. Surface glossy.

Pronotum. Transverse, convex, widest about in middle, base much wider than apex. Lateral margin posteriorly almost straight, slightly oblique. Posterior angles rectangular, feebly produced over lateral part of base. Carina at posterior angle elongate, rather oblique, slightly incurved. Anterior transverse sulcus deep, barely interrupted. Posterior transverse sulcus very deep, interrupted by a large, deep fovea. Anterior lateral seta situated slightly behind anterior third of margin. Microreticulation completely absent, surface highly glossy.

Elytra. Rather short, highly convex, egg-shaped, widest about in middle. Lateral border evenly curved, extremely finely serrate and pilose.

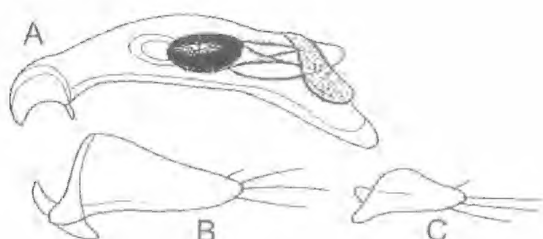


FIG. 1. *Phillipis unistriata* sp. nov. A, aedeagus, and B, C, parameres; scale bar = 0.25mm.

Sutural stria very faintly crenulate. Only inner striae in basal half perceptible as rows of extremely superficial punctures, outer striae absent, though all striae except for sutural one barely perceptible. Sutural interval basally slightly convex, 8th stria deeply impressed, punctate-crenulate, barely attaining posterior marginal pore. Recurrent striae rather evenly curved, anteriorly free. Anterior discal pore in anterior third, posterior pore slightly in front of posterior third. Microreticulation absent on disk, present though highly superficial at base, composed of transverse meshes. Surface glossy. Wings slightly shortened.

Lower surface Metepisternum slightly longer than wide.

Male genitalia. Genital ring slightly asymmetric, triangular, apex rather elongate. Aedeagus moderately elongate, lower surface basally straight, gently curved to apex, apex fairly short, widely rounded off. Both parameres 4-setose.

Female genitalia. Unknown.

DISTRIBUTION. Mt Elliot near Townsville, N Queensland. Known only from type locality.

HABITAT. Sampled by Berlese extraction from rainforest litter at 1000m.

RELATIONSHIP This species belongs to the *striata*-group of species and is perhaps nearest related to *P. tribulationis* Baehr and *P. thompsoni* Baehr.

***Phillipis striatoides* sp. nov.**
(Fig. 2B)

ETYMOLOGY. Like *striata*.

MATERIAL EXAMINED. HOLOTYPE: ♀, NEQ; 16°56'S 145°51'E, Mt Murray Prior, 31 Oct 1995, 770m, Monteith & Cook, Pyrethrum, trees & rocks (QMT 93347).

DIAGNOSIS. Rather small, short and wide, markedly convex species with s-shaped fascia in posterior half of elytra. Easily distinguished from species with similar elytral pattern by well-developed outer striae but rather depressed intervals and by weak microreticulation of the elytra. Further distinguished from most similar *P. striata* Baehr by wider pronotum with more convex margins and narrower base, and by considerably shorter and more convex elytra.

DESCRIPTION. *Measurements.* Length 2.15mm, width 1.08mm. Ratios: width pronotum/head: 1.50; width/length of pronotum: 1.59; width base/apex of pronotum: 1.41; width widest diameter/base of pronotum: 1.08; length/width of elytra: 1.27.

Colour. Dark piceous, pronotum and apex of elytra very slightly lighter. Elytra with a well-defined, contrasting, oblique, s-shaped, light reddish fascia in posterior 2/5, medially attaining 2nd stria. Legs yellow.

Head. Median antennomeres c. 1.3 x as long as wide. Microreticulation distinct on labrum and anterior border of clypeus, superficial on frons, absent on vertex, about isodiametric. Surface glossy.

Pronotum. Transverse, convex, widest about in middle, base much wider than apex. Lateral margin posteriorly almost straight, slightly oblique. Posterior angles rectangular, feebly produced over lateral part of base. Carina at posterior angle elongate, rather oblique, slightly incurved. Anterior transverse sulcus deep, barely interrupted. Posterior transverse sulcus very deep, interrupted by a large, deep fovea. Anterior lateral seta situated slightly behind anterior third of margin. Microreticulation completely absent, surface highly glossy.

Elytra. Rather short, highly convex, egg-shaped, widest about in middle. Lateral border evenly curved, extremely finely serrate and pilose. Sutural stria very faintly crenulate. All striae distinct and marked by rows of punctures, two inner striae in basal half even slightly impressed. Four to five inner intervals at least basally slightly convex. 8th stria deeply impressed, punctate-crenulate, barely attaining posterior marginal pore. Recurrent striae rather evenly curved, anteriorly meeting 3rd stria. Anterior discal pore in anterior third, posterior pore slightly in front of posterior third. Microreticulation present though highly superficial, best seen from laterally, composed of transverse

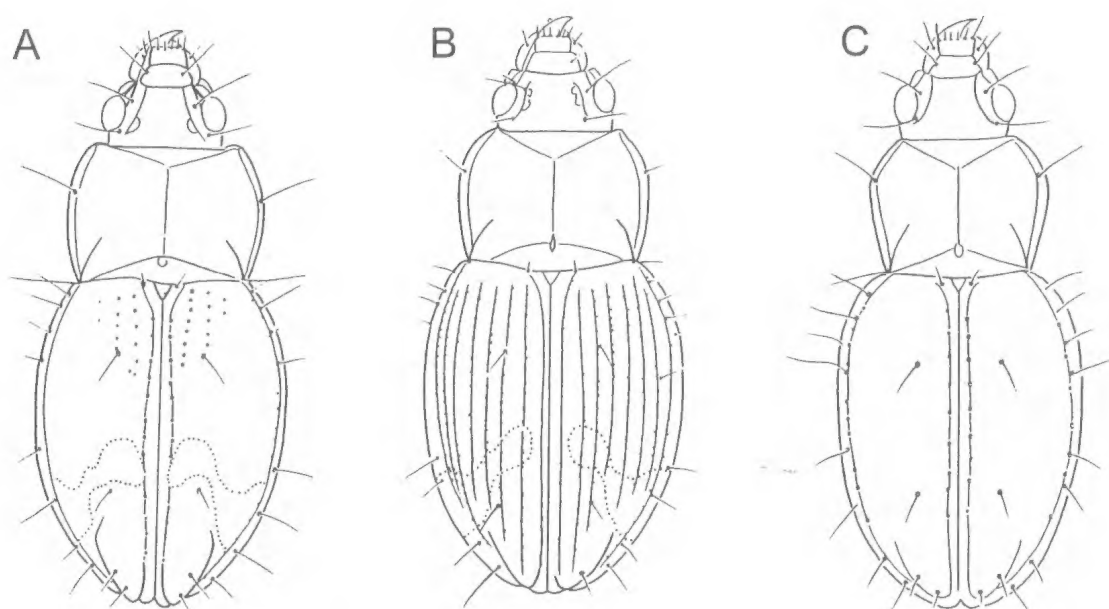


FIG. 2. Habitus. A, *Philipis unistriata* sp. nov. B, *Philipis striatoides* sp. nov. C, *Philipis inexpectata* sp. nov. Lengths: 2.15mm; 2.15mm; 2.55mm.

meshes. Surface glossy. Wings slightly shortened.

Lower surface. Metepisternum slightly longer than wide.

Male genitalia. Unknown.

Female genitalia. Similar to other species of the *striata*-group.

DISTRIBUTION. Mt. Murray Prior near Cairns, north Queensland. Known only from type locality.

HABITAT. Sampled by pyrethrum knockdown on mossy tree trunks or rocks in rainforest at 770m. Collected end of October.

RELATIONSHIP. This species belongs to the *striata* group of species and is nearest related to *P. striata* Baehr.

***Philipis inexpectata* sp. nov.**
(Fig. 2C)

ETYMOLOGY. The name refers to the unexpected occurrence of this species in New South Wales.

MATERIAL EXAMINED. HOLOTYPE: ♀, Gibraltar Range Nat. Park, NSW 30 Mar 1980, G. B. Monteith Pyrethrum/*Xanthorrhoea* (QMT 93346).

DIAGNOSIS. Rather large, elongate, convex, rufo-piceous species without any elytral pattern. Easily distinguished from all other unicolourous

species by complete absence of all elytral striae except for the sutural stria. Further distinguished from most similar *P. unicolor* Baehr and *P. atra* Baehr by straight lateral margin of pronotum in basal half.

DESCRIPTION. *Measurements.* Length: 2.55mm; width: 1.20mm. Ratios: width pronotum/head: 1.53; width/length of pronotum: 1.45; width base/apex of pronotum: 1.39; width widest diameter/base of pronotum: 1.09; length/width of elytra: 1.35.

Colour. Reddish piceous, head and pronotum slightly darker than elytra. Elytra without any distinct pattern. Mouth parts, three basal antennomeres, and legs yellow.

Head. Median antennomeres c. 1.3 x as long as wide. Microreticulation distinct on labrum, superficial on anterior border of clypeus, absent on frons and vertex, about isodiametric. Surface highly glossy.

Pronotum. Transverse, convex, widest about in middle, base much wider than apex. Lateral margin posteriorly straight, even very faintly concave, oblique. Posterior angles rectangular, very feebly produced over lateral part of base. Carina at posterior angle elongate, almost straight, only anteriorly slightly incurved. Anterior transverse sulcus deep, barely interrupted. Posterior transverse sulcus very

deep, interrupted by a large, deep fovea. Anterior lateral seta situated slightly behind anterior third of margin. Microreticulation completely absent, surface highly glossy.

Elytra. Rather elongate, highly convex, egg-shaped, widest about in middle. Lateral border evenly curved, not serrate nor pilose. Striae completely absent except for sutural stria that is deeply impressed and in anterior half also punctate-crenulate. 8th stria deeply impressed, punctate-crenulate, just attaining the posterior pore of the anterior series of marginal pores. Recurrent striae rather evenly curved. Anterior discal pore in anterior third, posterior pore slightly in front of posterior third, both deep and punctiform. Microreticulation completely absent. Surface highly glossy. Wings slightly shortened.

Lower surface. Metepisternum slightly longer than wide.

Male genitalia. Unknown.

Female genitalia. Similar to other species of *Philipis*.

Variation. Unknown.

DISTRIBUTION. Gibraltar Range in northern New South Wales. Known only from type locality.

HABITAT. Sampled by pyrethrum knockdown on *Xanthorrhoea*, according to label. Altitude not recorded, though probably on or near top of range. Collected end of March.

RELATIONSHIP. The species belongs to the *laevis*-group of species and is probably nearest related to *P. subtropica* Baehr.

RECOGNITION. For recognition of the new species the key in my revision (Baehr, 1995) can be used. *P. inexpectata* will key out at couplet 2, for identification of *P. striatoides* sp. nov. follow on to couplet 17, and for *P. unistriata* follow on to couplet 19. These couplets then must be altered as follows:

2. Rather short, dorsally convex species. Aedeagus as in fig. 4D-E (Baehr 1995) or unknown 3
- Rather elongate and depressed species. Aedeagus as in fig. 4C (Baehr 1995) or unknown 4
3. Lateral borders of pronotum convex throughout, though sometimes irregularly convex. At least traces of additional striae (apart from sutural stria) present. Aedeagus as in fig. 4D-E (Baehr 1995). Mountains of Queensland north of Eungella Range. 4a

Lateral borders of pronotum posteriorly straight. Only sutural stria present. Aedeagus unknown. Gibraltar Range, northern New South Wales *inexpectata*

4a. = 4 in Baehr (1995).

17. Microreticulation of elytra weak, surface glossy. Aedeagus, fig. 5B (Baehr 1995), or unknown 17a

Microreticulation of elytra distinct, surface rather dull. Aedeagus unknown. Bellenden Ker Range at 1000m *reticulata*

17a. Elytra longer and less convex, ratio length/width >1.32. Striae not impressed, intervals not convex. Base of pronotum wider, ratio base/apex >1.50. Aedeagus, fig. 5B (Baehr 1995). Cape Tribulation area below 150m *striata*

Elytra shorter and more convex, length/width 1.27. Inner striae slightly impressed, intervals slightly convex. Base of pronotum narrower, ratio base/apex 1.41. Aedeagus unknown. Mt. Murray Prior near Cairns at 770m *striatoides*

19. Smaller species, body length <2.15mm, and base of pronotum rather narrow, ratio base/apex <1.42. Aedeagus, fig. 5E (Baehr 1995) or Fig. 1 19a

Commonly larger species, body length >2.20mm, or base of pronotum wider, ratio base/apex >1.45. Aedeagus as in figs 5F, 6A (Baehr 1995). 20

19a. Pronotum narrower, ratio width/length <1.53. Elytra slightly longer, ratio length/width >1.31. Transverse macula less oblique and sinuate, fig. 13E (Baehr 1995). Both parameres 5-setose, see fig 5E (Baehr 1995). Mountains west of Cape Tribulation and Windsor Tableland above 700m *tribulationis*

Pronotum wider, ratio width/length 1.67. Elytra slightly shorter, ratio length/width 1.29. Transverse macula more oblique and sinuate, fig. 2A. Both parameres 4-setose, fig. 1. Mt. Elliot near Townsville, at 1000m *unistriata*

REMARKS. The additional records mentioned in this paper reveal: 1) ranges of known species probably are well known, because ample additional collecting efforts have not much altered the recorded ranges. 2) When sampling still unworked mountain tops the chance to detect additional species is substantial, and further work will probably yield additional new species, probably even in quite large numbers. This may apply in particular to the many yet unworked mountain tops in the southern tropical and the subtropical parts of eastern Queensland, between Mt Elliot and the Lamington Plateau. The detection of an additional new species in northern New South Wales supports this opinion.

Hence, the findings corroborate the idea that most species of *Philipis* in a way have been trapped on mountain tops where they occupy mostly very restricted ranges. The two new species, *P. unistriata* and *P. striatoides*, demonstrate that species widely separated geographically may be closely related. This,

again, demonstrates the very recent taxonomic diversification of this old stock.

An uncommon occurrence would be the observation of *P. inexpectata* living on grass-trees, *Xanthorrhoea*, if the label record is reliable and the single recorded specimen is not a straggler. This would mean that not all species of *Philipis* occur in rain forest.

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LITERATURE CITED

- BAEHR, M. 1995. Revision of *Philipis* (Coleoptera: Carabidae: Bembidiinae), a genus of arboreal Tachyine beetles from the rainforests of eastern Australia. Taxonomy, phylogeny, and biogeography. *Memoirs of the Queensland Museum* 38: 315-381.



TWO NEW SPECIES OF *SLOANEANA* CSIKI FROM SOUTHERN QUEENSLAND (COLEOPTERA, CARABIDAE, MERIZODINAE)

MARTIN BAEHR

Bachr, M. 2002 5 31: Two new species of *Sloaneana* Csiki from southern Queensland (Coleoptera, Carabidae, Merizodinae). *Memoirs of the Queensland Museum* 48(1): 9-15. Brisbane. ISSN 0079-8835.

Sloaneana lamingtonensis sp. nov. and *S. similis* sp. nov. are described from Springbrook and Lamington Plateaus near the Queensland/New South Wales border. They are distinguished from the known species of *Sloaneana*, *S. tasmaniae* (Sloane), by pronotum with wide base, rectangular basal angles, and distinct latero-apical ridge, and by more ovoid, 3- or 4-punctate elytra. Both new species are mainly distinguished *inter se* by their different aedeagi, and by larger size, and deeper, more coarsely punctate elytra in *S. lamingtonensis*. The new records extend the range of Merizodinae in Australia into the subtropics. A new record of the Tasmanian merizodine *Pterocyrtus rubescens* (Sloane) from Mt. Field is also dealt with. Probably this is the second record of this species since description. □ *Coleoptera, Carabidae, Merizodinae, Queensland, new species.*

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The few Australian species of the carabid Merizodinae have a southern distribution with most species occurring in Tasmania and but two on the mainland where they were not yet recorded further north than the Australian Alps in eastern Victoria (*Pterocyrtus truncaticollis* Sloane) and southern NSW (*Sloaneana tasmaniae* Sloane = *victoriae* Sloane) (Moore et al., 1987). Hence, Merizodinae are typical representatives of the cold adapted Bassian faunal element and are believed to belong to the circumpolar so-called Gondwanan faunal element that today persists in SE Australia, New Zealand, and southernmost South America.

More surprising was discovery of additional species of *Sloaneana* Csiki (replacement name for *Brachydema* Sloane) as far north as Lamington Plateau in SE Queensland. There, in 1982 I collected a single specimen of an apparently new species which I was reluctant to describe, because it was a female. Recently, G. Monteith of the Queensland Museum informed me that he had collected a small series at different localities on Lamington Plateau during his ample program of pyrethrum fogging tree trunks and logs on mountain tops along eastern Queensland. Now altogether 7 specimens are at hand, and although they externally look quite similar, closer examination shows that they belong to two different species.

Although Lamington Plateau is within the subtropics, both new species apparently occur only above about 1000 m and hence, in the cool

temperate rain forest on the plateau where conditions are still fairly 'Bassian'. One specimen has been collected on *Nothofagus* which is evidence of preference for cool environments.

METHODS

After dissection the male genitalia were cleaned for a while in hot 4% KOH.

MEASUREMENTS

Measurements have been made under a stereo microscope by use of an ocular micrometer. Length has been measured from apex of labrum to apex of elytra. Length of pronotum was taken along midline. Measurements, therefore, may slightly differ from that of other authors.

MATERIAL

Types are in the Queensland Museum, Brisbane (QMB) except a paratype of each new species in the Zoologische Staatssammlung, München (CBM).

SYSTEMATICS

Sloaneana tasmaniae (Sloane) (Fig. 1)

Sloane, 1915: 452 (*Brachydema*); 1920: 130; Moore et al. 1987: 123

Brachydema victoriae Sloane, 1915: 452.

MATERIAL EXAMINED. 2 ♂♂, Hobart, Tasmania, J. J. Walker (BMNH); ♀, Lake St. Clair, Tas, 12.10.1972, M. Bachr (CBM); ♂, Tas. Mt Field, Lyrebird Walk.

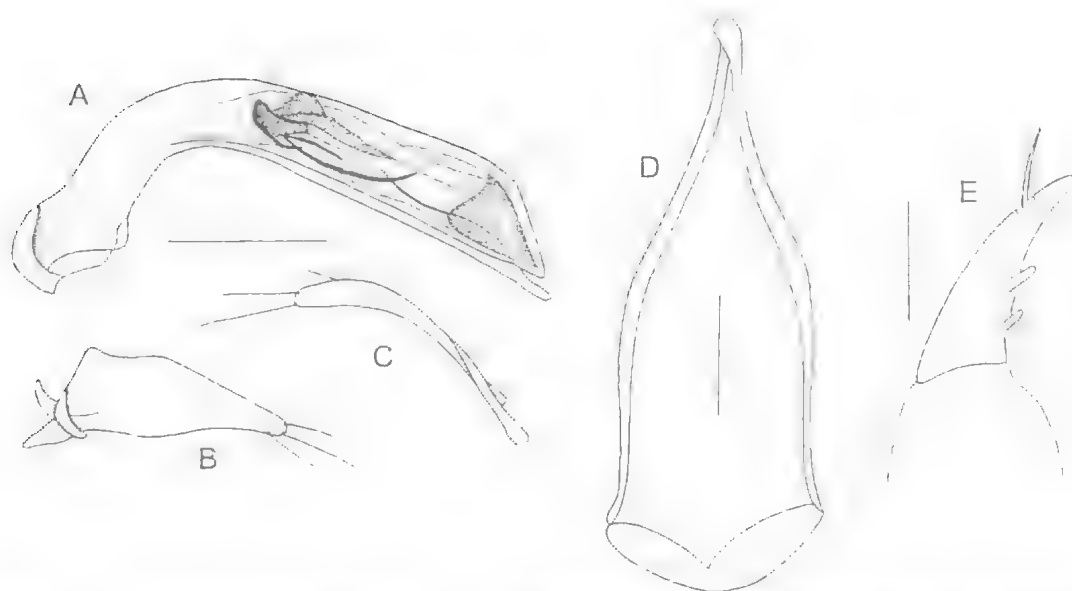


FIG. 1. *Sloaneana tasmaniae* (Sloane). Male A, aedeagus, B, C, parameres, and D, genital ring; scale bars = 0.25mm, E, female stylomere 2 and base of stylomere 1; scale bar = 0.1mm.

30.11.1998, leg. H. Pieper (CBM); ♀, Tas. Hartz Mt., 3.12.1998, leg. H. Pieper (CBM).

***Sloaneana lamingtonensis* sp. nov.**
(Figs 2, 3)

DESCRIPTION OF MALE AND FEMALE GENITALIA. *Male genitalia.* Genital ring narrow, elongate, almost symmetric, apex narrow, symmetric. Aedeagus narrow and elongate, sharply curved near base, lower surface straight, apex moderately short, straight. Orificium short. Internal sac rather complexly folded, with some narrow sclerites in basal part. Parameres large, very dissimilar, right paramere very narrow, elongate, left paramere large, rather triangular, moderately elongate. Left paramere with 3 elongate setae at apex, right paramere with 2 elongate setae and in one specimen with an additional shorter postapical seta.

Female genitalia. Apex of 1st stylomere asetose. 2nd stylomere elongate, narrow, with acute apex, with 2 rather small, widely spaced latero-ventral ensiform setae, with 2 elongate, attached, nematiform setae near apex that originate from an oblong pit, without dorso-median ensiform setae.

NOTE. For better discrimination between this and the following new species male and female genitalia of *B. tasmaniae* (Sloane) are figured for the first time, and some measurements and ratios are compared (Appendix 1).

MATERIAL EXAMINED. HOLOTYPE: ♂, SEQ: 28°15'S; 153°16'E Springbrook Repeater, 21 Dec 1996. 1000 m G. B. Monteith Pyrethrum, dead trees (QMT93095). PARATYPES: 2 ♀♀, SEQ: 28° 15'S; 153°16'E Springbrook Repeater 6 Apr 1995 G. B. Monteith, Pyrethrum Tree trunks, 1000 m (CBM, QMT93096); ♂, SEQ: 28°15'S; 153°12'E Mt. Hobwee summit 2 Dec 1995, 1150 m G. B. Monteith Pyrethrum, trees (QMT93098); 1 ♀, Bithongabel Lamington N.P., Q. 8 Oct 1979 G. Monteith/ Pyrethrum on *Nothofagus* (QMT93097).

DIAGNOSIS. Comparatively large species with angulate basal pronotal angles, distinguished from closely related *S. similis* sp. nov. by larger size, quadripunctate elytra, deeper and more distinctly punctate elytral striae, and downcurved apex of aedeagus.

DESCRIPTION. Measurements. Length: 3.65–3.85mm; width: 1.65–1.80mm; ratio width/length of pronotum: 1.51–1.56; ratio base/apex of pronotum: 1.65–1.69; ratio width of pronotum/width of head: 1.72–1.76; ratio length/width of elytra: 1.34–1.38; ratio width of elytra/width of pronotum: 1.24–1.26.

Colour: Piceous-black to black, with more or less distinct metallic lustre. Lateral margins of pronotum and elytra narrowly reddish, Mandibles and palpi reddish, penultimate

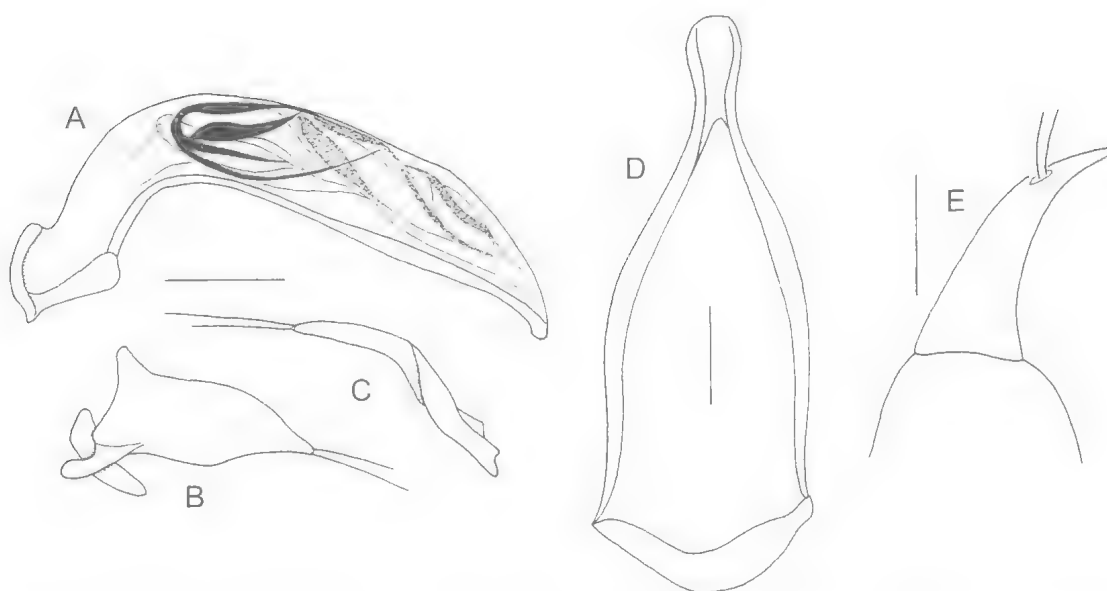


FIG. 2. *Sloaneana lamingtonensis* sp. nov. Male A, aedeagus, B, C, parameres, and D, genital ring; scale bars = 0.25mm. E, female stylomere 2 and base of stylomere 1; scale bar = 0.1mm.

palpomeres darker. Three basal antennomeres light reddish, rest piceous. Legs light reddish, femora in parts and external surface of tibiae slightly darker. Lower surface piceous, epipleurae reddish.

Head. Rather narrow in comparison with prothorax. Frons convex, with some shallow transverse furrows. Frontal furrows deep, semicircular, margins more or less crenulate according to depth of transverse furrows. Eyes large, moderately protruding, with small, obliquely convex orbits. Clypeo-frontal suture more or less distinct. Anterior margin of clypeus straight, bisetose. Labrum short and wide, apex straight, 6-setose. Mandibles moderate, acute. Terminal palpomeres elongate, acute, impilose. Mentum with obtuse, triangular tooth, bisetose. Gula quadrisetose. Glossa narrow, bisetose, paraglossae barely surpassing glossa. Antenna rather short, just surpassing base of pronotum, median antennomeres c. 1.5 x longer than wide, 3 basal antennomeres sparsely setose, densely setose from middle of 4th antennomere. Microreticulation distinct on labrum and apical half of clypeus, in some specimens also on vertex, rather superficial or almost wanting on frons, about isodiametric. Surface impunctate, impilose, rather glossy.

Pronotum. Wide, somewhat triangular. Apex considerably wider than base, barely to very

feebly concave, anterior angles broadly rounded, barely produced. Sides almost evenly rounded, widest shortly in front of base. Basal angles angulate, though about 100°. Base almost straight. Apex more or less distinctly bordered, lateral margins markedly bordered, border widened in apical half. Base laterally thickly bordered, border in middle highly superficial. Lateral channel rather narrow throughout. Disk evenly convex. Median line distinct, fairly impressed, complete. Anterior transverse sulcus very shallow, prebasal sulcus laterally close to basal margin, in middle convex, fairly deep. Basal grooves wide fairly deep, oblique, separated from lateral margin by a wide, conspicuous, convex hump. Anterior marginal seta situated in anterior 2/5, posterior marginal seta situated near basal angle. Both setae slightly removed from margin. Microreticulation more or less superficial, apparently less distinct in males, irregularly transverse. Surface almost impunctate, impilose, smooth, fairly glossy.

Elytra. Moderately short and wide, about oviform, widest about at middle, moderately convex. Humeri angulate, though not dentate, sides moderately, almost evenly convex, apex convex, without any sinuation. Marginal channel narrow throughout. In apical 1/4 with an externally careniform internal plica. Epipleurae distinctly crossed near apex. All striae visible,

though only sutural stria well impressed, other striae not or barely impressed, visible as rows of faint punctures. Sutural stria distinctly punctate, almost crenulate. Scutellary pore present, scutellary stria indistinct, consisting of few widely spaced, shallow punctures. Behind scutellum with a shallow, oblique groove. 3rd interval with four discal punctures, all situated near 3rd stria. Marginal series consisting of 8-9 setiferous punctures, series widely separated in middle. Also with a setiferous puncture inside apical plica at end of 5th stria, and another puncture near apex at end of 3rd stria. Microreticulation more or less distinct, in males more superficial than in females, fairly transverse. Surface impunctate, moderately to fairly glossy. Posterior wings slightly shorter than elytra.

Lower surface. Prosternum impilose. Lower surface impilose. Metepisternum about as long as wide at apex. Terminal abdominal sternum in male bisetose, in female quadrisetose.

Legs. Fairly elongate, especially tarsi rather slender and elongate. Two basal tarsomeres of male protarsus slightly widened and biserially squamose.

Male genitalia. Genital ring narrow, elongate, almost symmetric, apex wide, somewhat spoon-shaped. Aedeagus narrow and elongate, sharply curved near base, lower surface almost straight, apex short, distinctly bent down. Orificium short. Internal sac rather complexly folded, with some narrow sclerites in basal part. Parameres large, very dissimilar, right paramere very narrow, elongate, left paramere large, rather triangular, comparatively short. Both parameres with two elongate setae at apex.

Female genitalia. Apex of 1st stylomere asetose. 2nd stylomere elongate, narrow, with acute apex, without latero-ventral and dorso-median ensiform setae, with two elongate, nematiform setae near apex that originate from an oblong pit.

Variation. Some variation noted in relative shape of pronotum and in microreticulation of surface. With respect to the small number of available specimens it is so far unknown, to what extent this is due to sexual variation.

DISTRIBUTION. Lamington Plateau near Queensland/New South Wales border, southeastern Queensland. Known only from that range.

HABITS. This species lives on tree trunks in montane rain forest above about 1000m. One

specimen was sampled from *Nothofagus* which is evidence that the species also occurs in temperate (*Nothofagus*) rain forest that covers the highest tops of Lamington Plateau.

ETYMOLOGY. Refers to the species range.

***Sloaneana similis* sp. nov.**

(Fig. 3)

MATERIAL EXAMINED. HOLOTYPE: ♂, SEQ: 28°15'S; 153°16'E Springbrook Repeater, 21 Dec 1996. 1000m G.B. Monteith Pyrethrum, dead trees (QMT93094). PARATYPE: ♀, Lamington NP, O'Reillys. 1000m, 1.2.1982 M. Bachr (CBM).

DIAGNOSIS. Small species with angulate basal pronotal angles, distinguished from closely related *S. lamingtonensis* sp. nov. by smaller size, tripunctate elytra, shallower and almost impunctate elytral striae, and straight apex of aedeagus.

DESCRIPTION. *Measurements.* Length: 3.05-3.25mm; width: 1.4-1.5mm; ratio width/length of pronotum: 1.49-1.53; ratio base/apex of pronotum: 1.65-1.68; ratio width of pronotum/width of head: 1.65-1.70; ratio length/width of elytra: 1.36-1.39; ratio width of elytra/width of pronotum: 1.26-1.28.

Colour. Piceous-black to black, with more or less distinct metallic lustre. Lateral margins of pronotum and elytra narrowly reddish. Mandibles and palpi reddish, penultimate palpomeres darker. Three basal antennomeres light reddish, rest piceous. Legs light reddish, femora in parts and basal half of external surface of tibiae slightly darker. Lower surface piceous, epipleurae reddish.

Head. Rather narrow in comparison with prothorax. Frons convex, with some extremely shallow transverse furrows. Frontal furrows deep, semicircular, margins barely crenulate. Eyes large, moderately protruding, with small, obliquely convex orbits. Clypeo-frontal suture rather distinct. Anterior margin of clypeus straight, bisetose. Labrum short and wide, apex straight, 6-setose. Mandibles moderate, acute. Terminal palpomeres elongate, acute, impilose. Mentum with obtuse, triangular tooth, bisetose. Gula quadrisetose. Glossa narrow, bisetose, paraglossae slightly surpassing glossa. Antenna rather short, just surpassing base of pronotum, median antennomeres c. 1.5 x longer than wide, three basal antennomeres sparsely setose, densely setose from middle of 4th antennomere. Microreticulation distinct on labrum and apical half of clypeus, very superficial or almost

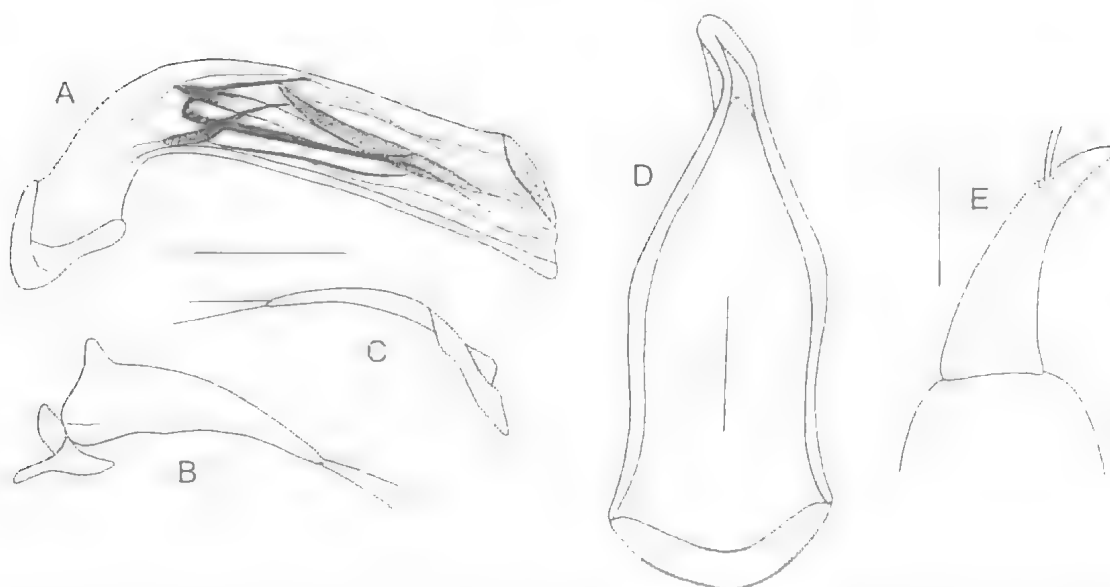


FIG. 3. *Sloaneana similis* sp. nov. Male A, aedeagus, B, C, parameres, and D, genital ring; scale bars = 0.25mm. E, female stylomere 2 and base of stylomere 1; scale bar = 0.1mm.

wanting on frons, about isodiametric. Surface impunctate, impilose, rather glossy.

Pronotum. Wide, somewhat triangular. Apex considerably wider than base, barely concave, anterior angles broadly rounded, barely produced. Sides almost evenly rounded, widest shortly in front of base. Basal angles angulate, though about 100° . Base almost straight. Apex rather distinctly bordered, lateral margins markedly bordered, border widened in apical half. Base laterally thickly bordered, border in middle highly superficial. Lateral channel rather narrow throughout. Disk evenly convex. Median line distinct, fairly impressed, complete. Anterior transverse sulcus very shallow, prebasal sulcus laterally close to basal margin, in middle convex, fairly deep. Basal grooves wide fairly deep, oblique, separated from lateral margin by a wide, conspicuous, convex hump. Anterior marginal seta situated at anterior $2/5$, posterior marginal seta situated near basal angle. Both setae slightly removed from margin. Microreticulation absent, surface almost impunctate, impilose, smooth, glossy.

Elytra. Moderately short and wide, about oviform, widest about at middle, moderately convex. Humeri angulate, though not dentate, sides moderately, almost evenly convex, apex convex, without any sinuation. Marginal channel narrow throughout. In apical $1/4$ with an

externally careniform internal plica. Epipleurae distinctly crossed near apex. All striae visible, though only sutural stria slightly impressed, other striae not impressed, visible as extremely superficial rows of faint punctures. Sutural stria barely punctate, not crenulate. Scutellary pore present, scutellary stria absent. Behind scutellum with a shallow, oblique groove. 3rd interval with three discal punctures, all situated near 3rd stria. Marginal series consisting of 8-9 setiferous punctures, series widely separated in middle. Also with a setiferous puncture inside apical plica at end of 5th stria, and another puncture near apex at end of 3rd stria. Microreticulation absent in both sexes. Surface impunctate, glossy. Posterior wings slightly shorter than elytra.

Lower surface. Prosternum impilose. Lower surface impilose. Metepisternum slightly shorter than wide at apex. Terminal abdominal sternum in male bisetose, in female quadrisetose.

Legs. Fairly elongate, especially tarsi rather slender and elongate. Two basal tarsomeres of male protarsus slightly widened and biserially squamose.

Male genitalia. Genital ring narrow, elongate, rather symmetric, laterally distinctly incurved, apex rather narrow, slightly asymmetric. Aedeagus rather narrow and elongate, sharply curved near base, lower surface straight, apex very short, straight. Orificium short. Internal sac



FIG. 7. *Sloaneana lamingtonensis* sp. nov. Habitus. Length: 3.65mm.

rather complexly folded, with some narrow sclerites in basal part. Parameres large, elongate, very dissimilar, right paramere extremely narrow, left paramere large, rather triangular, comparatively elongate. Both parameres with two elongate setae at apex.

Female genitalia. Apex of 1st stylomere asetose. 2nd stylomere elongate, narrow, with acute apex, without latero-ventral and dorso-median ensiform setae, with two elongate, nematiform setae near apex that originate from an oblong pit.

Variation. Very little variation noted. In the female paratype external striae of elytra even less distinct than in male holotype.

DISTRIBUTION. Lamington and Springbrook Plateaus near the Queensland/NSW border, SE Queensland.

HABITS. This species lives on tree trunks in montane rain forest above about 1000m. The paratype was collected in subtropical montane rain forest; the holotype might have been collected either in rain forest or in *Nothofagus* forest.

ETYMOLOGY. Similar to *S. lamingtonensis* sp. nov.

REMARKS. The occurrence of two species of the southern genus *Sloaneana* in SE Queensland indicates a considerable range extension of the genus and generally of the subfamily Merizodinae to the north through the whole of New South Wales. The occurrence of so-called Antarctic or Bassian faunal elements in subtropical or even tropical latitudes is not too unusual, provided the environments are of 'Bassian' type. See for example the existence of an - undescribed - migadopine species in North Queensland (G. Monteith, pers. inform.). Why should Bassian faunal elements not exist in Bassian *Nothofagus* forests on the top of Lamington Plateau?

However, it is extraordinary that this limited area is the home of two very similar, sympatric and most probably even syntopic species, whereas the whole of Tasmania, SE Victoria and southernmost NSW is inhabited by only one species of *Sloaneana*. As both new species are externally very similar, colonization of Lamington plateau by two different stocks of *Sloaneana* is very unlikely. Hence, the species probably have evolved by sympatric evolution within their present range.

This hypothesis may be tested in future, perhaps through further discovery of *Sloaneana* in NSW.

KEY TO THE SPECIES OF *SLOANEANA* CSIKI

1. Pronotum markedly curved inwards towards basal angle, basal angle obtuse, posterior lateral seta slightly removed from lateral margin; pronotum without conspicuous boss in basal angle, transverse basal sulcus indistinct, not sharply impressed; elytra bipunctate; apex of aedeagus narrow, straight (Fig. 1), neither short and compact (Fig. 3), nor downcurved (Fig. 2); female stylomere 2 with two ventro-lateral ensiform setae (Fig. 1). Tasmania, E Victoria, adjacent SE NSW
 *tasmaniae* (Sloane)
- Pronotum not much curved inwards towards basal angle, basal angle angulate, posterior lateral seta at lateral margin; pronotum with conspicuous fold in basal angle, transverse basal sulcus distinct, sharply impressed (Fig. 3); elytra tripunctate or quadripunctate; apex of aedeagus either short and compact (Fig. 3), or downcurved (Fig. 2); female stylomere 2 without ventro-lateral ensiform setae (Figs 5, 6). Lamington and Springbrook Plateaus, SE Queensland 2
2. Larger species, body length >3.6mm; elytra quadripunctate, striae more deeply impressed, distinctly punctate; apex of aedeagus downcurved, both parameres shorter and wider (Fig. 2).
 *lamingtonensis* sp. nov.
- Smaller species, body length <3.3mm; elytra tripunctate, striae barely impressed, almost impunctate; apex of

aedeagus short and straight, both parameres longer and narrower (Fig. 3) *similis* sp. nov.

ACKNOWLEDGEMENTS

My sincere thanks are due to Dr G.B. Monteith, Brisbane, for stimulating work on the new species and for loan of most of the examined material, and to Dr H. Pieper, Kiel, for providing Tasmanian specimens, collected by him in 1998.

LITERATURE CITED

- MOORE, B. P., T. A. WEIR & J. E. PYKE. 1987. Rhysodidae and Carabidae. In: Zoological Catalogue of Australia, 4: 17-320. Australian Government Publishing Service, Canberra.
- SLOANE, T. G. 1920. The Carabidae of Tasmania. Proceedings of the Linnean Society of New South Wales 45: 113-178.

APPENDIX 1

For better comparison of the new species with *S. tasmaniae* (Sloane) the measurements and ratios of the three species are compiled in Table 1. From *S. tasmaniae* five specimens from Tasmania were at hand.

APPENDIX 2

A new record of the Tasmanian merizodine *Pterocyrtus rubescens* Sloane is now available. A single specimen was collected by H. Pieper (Kiel) at Mount Field in southwestern Tasmania (Mt Field, Lyrebird Walk, 20.11.1998). According to Moore et al. (1987) this species had been known only from the holotype. Hence, this is the second (published) record of this species since description (Sloane, 1920). The type locality is Waratah in northwestern Tasmania. *Pterocyrtus rubescens*, therefore, seems to be distributed more extensively in western Tasmania.

TABLE 1.

	N	Body length(mm)	Ratio width/length pronotum	Ratio width base/apex pronotum	Ratio width pronotum/head	Ratio length/width elytra	Ratio width elytra/pronotum
<i>tasmaniae</i>	5	4.1-4.4	1.45-1.48	1.67-1.73	1.87-1.91	1.36-1.39	1.16-1.18
<i>lamingtonensis</i>	5	3.65-3.85	1.51-1.56	1.65-1.69	1.72-1.76	1.34-1.38	1.24-1.26
<i>similis</i>	2	3.05-3.25	1.49-1.53	1.65-1.68	1.65-1.70	1.36-1.39	1.26-1.28

CHEENEETNUKIIDAE, A NEW MIDDLE DEVONIAN MURCHISONIROID GASTROPOD FAMILY, INCLUDING THE NEW GENERA *CHEENEETNUKIA* AND *ULUNGARATOCONCHA* BASED ON REPRESENTATIVES FROM ALASKA AND AUSTRALIA

ROBERT B. BLODGETT AND ALEX G. COOK

Blodgett, R.B. & Cook, A.G. 2002 5 31: Cheeneetnukiidae, a new Middle Devonian murchisoniroid gastropod family, including the new genera *Cheeneetnukia* and *Ulungaratoconcha* based on representatives from Alaska and Australia. *Memoirs of the Queensland Museum* 48(1): 17–28, Brisbane. ISSN 0079-8835.

Two new genera of murchisoniroid gastropods, *Cheeneetnukia* and *Ulungaratoconcha*, are established from the Middle Devonian (Eifelian and Givetian) strata of the Old World Realm and are placed in Cheeneetnukiidae fam. nov., belonging to Murchisonioida. Cheeneetnukiidae represent a distinctive group of Middle Devonian murchisonioids characterised by a squared-off (rectangular) whorl profile, a flattened vertical outer whorl surface with a broad, centrally situated selenizone which is bounded above and below by strong angulations, often in the form of flange-like projections. Strongly ornate (nodose or spinose) forms are common amongst the younger Givetian representatives of the family. The family underwent an explosive adaptive radiation of intricate and highly decorated forms that are restricted to the Middle Devonian (Eifelian and Givetian). The family is characteristic for warm tropical seaways of the Middle Devonian, and its representatives are known from Germany, various accreted Alaskan terranes (Farewell, Alexander and Arctic Alaska), northeastern Australia, Malaysia and southern China. Three new species are here described: 1) the type species of *Cheeneetnukia*, *C. frydai* from the Eifelian of Alaska, known from both the Cheeneetnuk Limestone of west-central Alaska (Nixon Fork subterrane of the Farewell terrane) and the Wadleigh Limestone from southeastern Alaska (Alexander terrane); 2) *C. australis* from the uppermost Dosey Limestone (early Givetian) of north Queensland, Australia; and 3) the type species of *Ulungaratoconcha*, *U. heidelbergi* from Eifelian strata of the Ulungarat Formation (Member A), northeastern Brooks Range, northeastern Alaska (Arctic Alaska terrane). □ *Devonian, Alaska, Australia, Gastropoda, Cheeneetnukiidae.*

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Murchisonioid gastropods underwent significant speciation during the Middle Devonian resulting in a plexus of unusual medium to large-sized, often nodose or spinose forms (Andree, 1928; Gruneberg, 1927; Paekelmann, 1922). This radiation was also mentioned by Knight et al. (1960: 1291) who in reference to *Murchisonia* stated: 'In Middle Devonian close relatives of the type species display a burst of forms with elaborate, in part bizarre, shapes and ornament quite incongruous with usual conservatism shown by genus'. Such bizarre murchisonioids characterise typical Old World Realm Middle Devonian (all Givetian in age) faunas in Europe (D'Archaic & DeVerneuil, 1842; Goldfuss, 1841–1844; Sandberger & Sandberger, 1850–1856; Whidborne, 1889–1892; Lotz, 1900; Kirchner, 1915; Heidelberg, 2001), southern China (Mansuy, 1912; Cook, pers. obs.) and to a lesser extent western Canada (Whiteaves, 1892)

and Australia (Cook & Camilleri, 1997). This unusually ornate group of murchisonioid gastropods is characterised by a distinctive, 'squared-off' rectangular whorl profile which clearly distinguishes it, and for which we erect Cheeneetnukiidae fam. nov. In the family, we establish *Cheeneetnukia* gen. nov. from S Alaska (Farewell and Alexander terranes) and NE Australia, and *Ulungaratoconcha* gen. nov. based on a NE Alaskan species, but which also includes many species recognised primarily in Europe. Both new genera are associated with the early phases of explosive adaptive radiation shown by the family. *Ulungaratoconcha* gen. nov. has been referred to in an earlier paper (Popov et al., 1994: 1214) simply as a 'new genus of murchisoniid gastropod'. In that same paper, devoted to the description of a new inarticulate brachiopod, this new gastropod genus was noted as occurring in the Ulungarat Formation of

Anderson (1991) of the Demarcation Point A-4 quadrangle, NE Brooks Range (Arctic Alaska terrane).

As noted above, *Cheeneetnukia* gen. nov. is also recognised in the uppermost Dosey Limestone (early Givetian) of N Queensland. Reconstructions of Scotese & McKerrow (1989) and Metcalfe (1996) show eastern Gondwana representing the farthest extent of the Old World Realm, with a significant distance across a proto-Pacific ocean (commonly called Panthalassa) to the Americas. The distribution of this new taxon is anomalous and suggests biogeographic pathways linking the Alaskan terranes (or blocks) to eastern Gondwana during the Middle Devonian. On the basis of Devonian biogeographic evidence (primarily brachiopods), as well as supporting evidence from other time intervals in the Early and Middle Palaeozoic, it has been recently suggested that the major Alaskan terranes with significant Devonian faunas such as the Farewell, Livengood, Arctic Alaska, and Alexander terranes, represent continental margin blocks which have been rifted apart from the Siberian palaeocontinent during Devonian time (Blodgett & Brease, 1997; Blodgett, 1997; Blodgett & Boucot, 1999; Garcia-Alcalde & Blodgett, 2001; Blodgett et al., in press).

SYSTEMATIC PALAEONTOLOGY

Type specimens of *Cheeneetnukia frydai* sp. nov. and *Ulungaratoconcha heidelbergeri* sp. nov. are deposited in the University of Alaska Museum (UAM) at Fairbanks, Alaska, and those of *C. australis* sp. nov. are deposited in the Queensland Museum (QMF), Brisbane.

Suborder MURCHISONIINA Cox & Knight, 1960
Superfamily MURCHISONIOIDEA Koken, 1896
Family MURCHISONIIDAE Koken, 1896

REMARKS. The Murchisoniidae (sensu Knight et al., 1960) is recognised as polyphyletic, as shown by recent protoconch studies of some of its constituent genera. The protoconch of the type species of *Murchisonia*, *M. bilineata* (Dechen, 1832), as well as those of closely related Middle Devonian species remains unknown; however, Frýda & Manda (1997) and Frýda (1999a) demonstrated an archaeogastropod type protoconch in a number of Early Devonian species of *Murchisonia* from the Prague Basin. In contrast, Nützel & Bandel (2000) demonstrated a caenogastropod type protoconch in members of their newly established Goniasmidae, including

Goniasma, *Stegocoelia*, and *Cerithioides*, which they transferred from the Murchisoniidae to the order Cerithimorpha of the subclass Caenogastropoda.

We regard all subgenera of *Murchisonia* recognised by Knight et al. (1960), as well as the subsequently established *Murchisonia* (*Ostioma*) Tassell, 1980, to be independent taxa worthy of generic rank within the Murchisoniidae. *Murchisonia* should be restricted to those species that are closely allied with the type species, *M. bilineata* (Dechen, 1832) from the Middle Devonian (Givetian) of Germany. *Murchisonia* has for over a century and a half served as 'catch-all' for a vast array of species characterised only in being relatively high-spired and possessing a selenizone. In light of the now obvious polyphyletic origin of many of its members, based on protoconch studies and the great diversity of teleoconch morphologies, we believe both *Murchisonia* and the Murchisoniidae are long overdue for intensive revision.

Family CHEENEETNUKIIDAE fam. nov.

DIAGNOSIS. Medium- to large-sized; whorl profile distinctly squared-off (rectangular), with a flat to moderately inclined upper whorl surface, below which is a vertical, flattened outer whorl surface bearing a broad, centrally situated selenizone; upper and lower boundaries of the outer whorl surface marked by strong angulations, often projecting abaxially as a flange; protuberances, spines, and nodes are commonly well developed.

REMARKS. The Cheeneetnukiidae is easily distinguished within the Murchisonioidea by its characteristically squared-off (rectangular) whorl profile. In other murchisonioids, the whorl profile is typically V-shaped or rounded. The type species of *Murchisonia*, *M. bilineata* (Dechen, 1832) from the Givetian of Germany, closely resembles members of the Cheeneetnukiidae but lacks the characteristic whorl profile of the new family. Based on the gross similarity of the Cheeneetnukiidae to the Murchisoniidae it is likely that both families are closely related and belong to the Archaeogastropoda, but knowledge of the protoconch is needed to corroborate this supposition. Cheeneetnukiidae and Murchisoniidae could share a common ancestor that gave rise to both highly diverse Devonian groups. Alternatively the presence of members of the Caenogastropoda and Heterobranchia in Devonian strata (Frýda &

Blodgett 2001, Frýda 2001) as well as shell homplasy in Devonian gastropods (Frýda, 1999b) complicate this interpretation. The adaptive significance of the distinctive whorl profile is presently unknown.

COMPOSITION. Members of the new family embrace the bizarre array of strange-shaped and ornate Middle Devonian *murchisonioids* that has previously been noted by earlier workers (Knight et al., 1960: 1291; Paetzelmann, 1922; Grüneberg, 1927; Andree, 1928). It is obvious that an explosive adaptive radiation occurred among members of this group, known only from Middle Devonian strata of the Old World Realm (Germany, Alaska, Australia, southern China). We distinguish two new genera within the family, *Cheeneetnukia* and *Ulungaratnconcha*, but believe that other species (nearly all assigned earlier to *Murchisonia*) within this plexus of distinctive *murchisonioids* will be assigned to separate genera pending further study.

Cheeneetnukia gen. nov.

TYPE SPECIES. *Cheeneetnukia frydai* gen. et sp. nov. from the upper Cheeneetnuk and Wadleigh Limestones, Alaska.

ETYMOLOGY. After the Cheeneetnuk Limestone.

DIAGNOSIS. Large, high-spired gradate, with a broad, flat subsutural ramp terminating at a projecting flange-like upper carina, the latter forming the shell periphery. Mid-whorl section vertical to weakly inclined inward, with a broad, flat selenizone bounded by two fine, weakly raised spiral threads. A lower, weaker carina forming the boundary between the mid-whorl section and the base. Succeeding whorls joining previous whorls at or just below lower carina. Base with narrow, but relatively deep umbilicus.

COMPARISON. The unusual whorl profile of *Cheeneetnukia* with its two strong angulations, the upper of which forms a prominent projecting flange-like carina and delimits a nearly flat, vertical outer whorl face, separates this genus from known *murchisonioid* genera. It is distinguished in its broad, gradate (step-like) shell from the only other genus assigned to the family, *Ulungaratnconcha* gen. nov., which possesses a narrowly acute shell.

COMPOSITION. *C. frydai* sp. nov.; *C. australis* sp. nov.

A third undescribed species may be present in the Givetian Ertang Formation of Guangxi,

China, but it is currently under review (Cook, pers. obs.). Another undescribed species, *Murchisonia* sp. C (Suntharalingam, 1968, fig. 12) from the Givetian Thye On beds near Kampar, Perak, Malaysia also appears to belong to *Cheeneetnukia*.

In addition, the following ornate Givetian species from Germany and England show some striking resemblance to *Cheeneetnukia*, notably in the broad spired, gradate form of the shell, and may prove to be closely related or descended from *Cheeneetnukia*. These include (using original author designation):

Murchisonia spinosa Phillips, 1841; Givetian of England and Germany.

Murchisonia seminodosa Grüneberg, 1927; Givetian of Germany.

Murchisonia coronata var. *turboides* Winterfeld, 1894; Givetian of Germany

Cheeneetnukia frydai sp. nov. (Figs 1-3)

TYPES. Holotype, UAM2639; paratypes, A-I, UAM 2640-2649. The types are from locality 83R18 in the McGrath A-5 quadrangle (Cheeneetnuk Limestone), west-central Alaska. A non-type specimen (UAM 2649) is also illustrated from USGS locality M1299-SID in the Craig D-4 quadrangle (Wadleigh Limestone), SE Alaska.

ETYMOLOGY. For Dr Jiri Frýda.

DIAGNOSIS. Upper angulation extremely strong, protruding, flange-like.

DESCRIPTION. Large, gradate, broad, high-spired shell; whorls up to 8 in teleoconch, protoconch not preserved; whorl profile distinctly 'squared-off' (rectangular) with two prominent angulations, one formed by strongly projecting carina situated at upper/outer whorl surface junction that forms the shell periphery, the other formed by less strongly projecting carina situated at outer/basal whorl face junction; sutures of variable strength, ranging from weak to strongly impressed, situated immediately beneath carina forming lower angulation; upper whorl face broad, commonly flat or rarely concave, horizontal or weakly inclined downward abaxially; outer whorl face flat to weakly concave, vertical to subvertical (slightly inclined inward basally); selenizone relatively broad, its surface smooth, slightly recessed, bearing weak lunulae, bordered by two fine spiral threads; base moderately convex, minutely phaneromphalous (but deep) in fully adult shells, cryptomphalous in juvenile specimens;

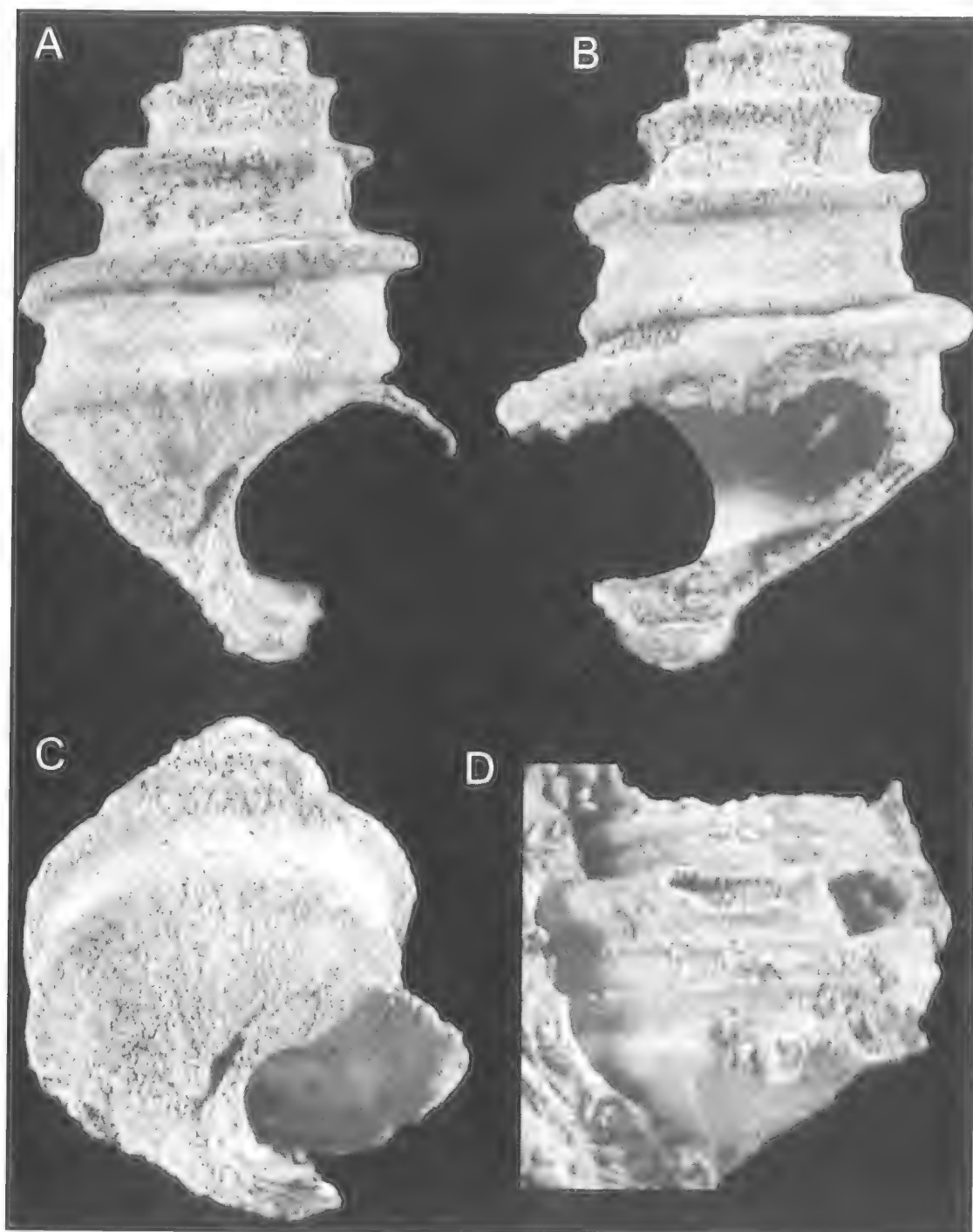


FIG. 1. A-D, *Cheeneetnukia frydai* gen. et sp. nov. A-C, Holotype UAM 2639, $\times 1.5$. A, apertural view; B, abapertural view; C, oblique basal view. D, Paratype A UAM 2640, $\times 2$, side view of shell fragment preserving penultimate and final whorls (note well developed centrally situated selenizone). Both specimens are from locality 79RB8 (USGS locality 10061-SD), McGrath A-5 quadrangle, west-central Alaska.

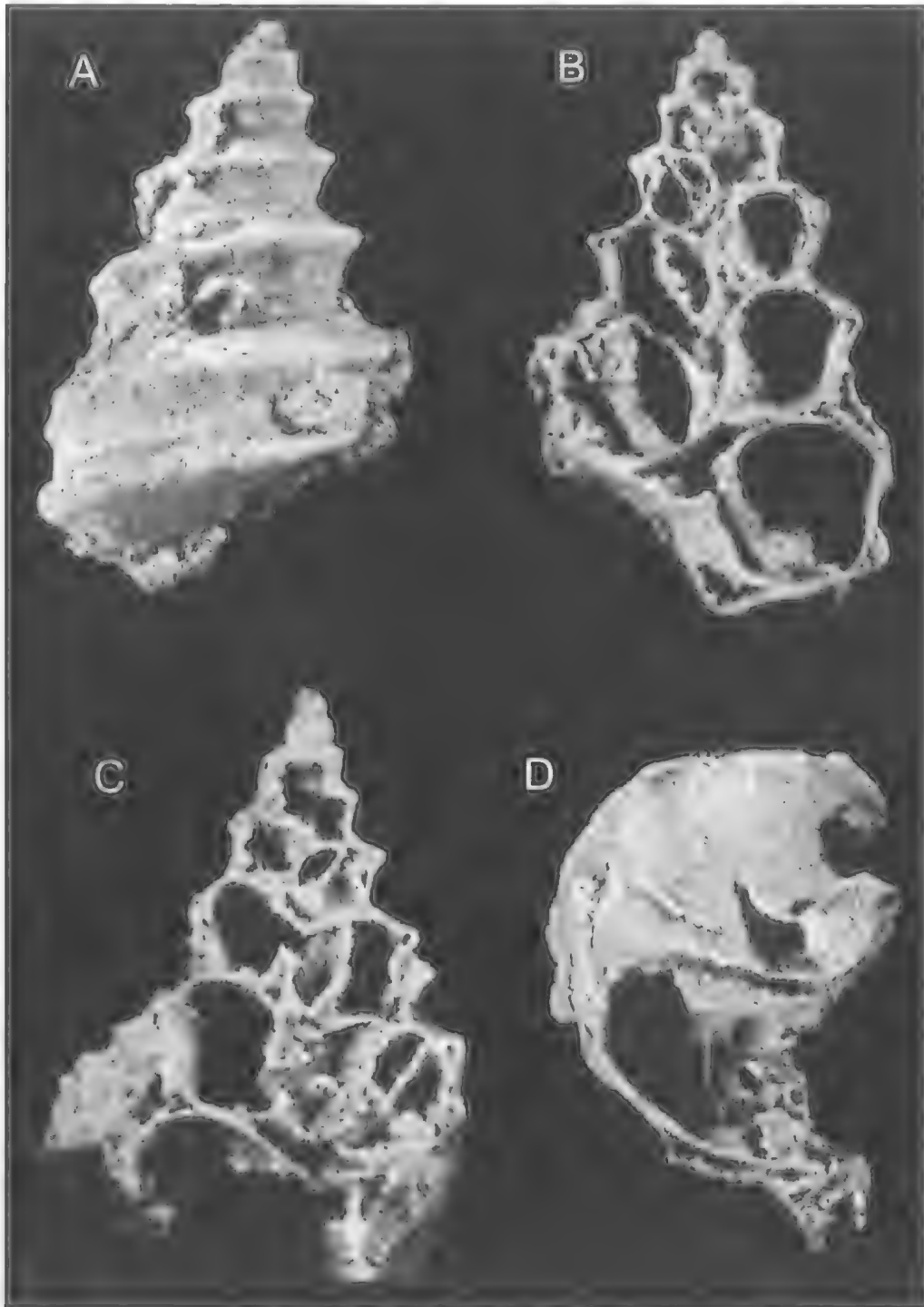


FIG. 2. A-D, *Cheeneetmukia frydai* gen. et sp. nov. A-B, Paratype B UAM 2641, $\times 2$. A, abapertural view; B, natural longitudinal section through same specimen. C, Paratype C UAM 2642, $\times 2$, longitudinal (natural) section (note distinctive external whorl typical for the Cheeneetmukiidae). D, Paratype D UAM 2643, $\times 1.5$, basal view. All specimens are from locality 79RB8 (USGS locality 10061-SD), McGrath A-5 quadrangle, west-central Alaska.

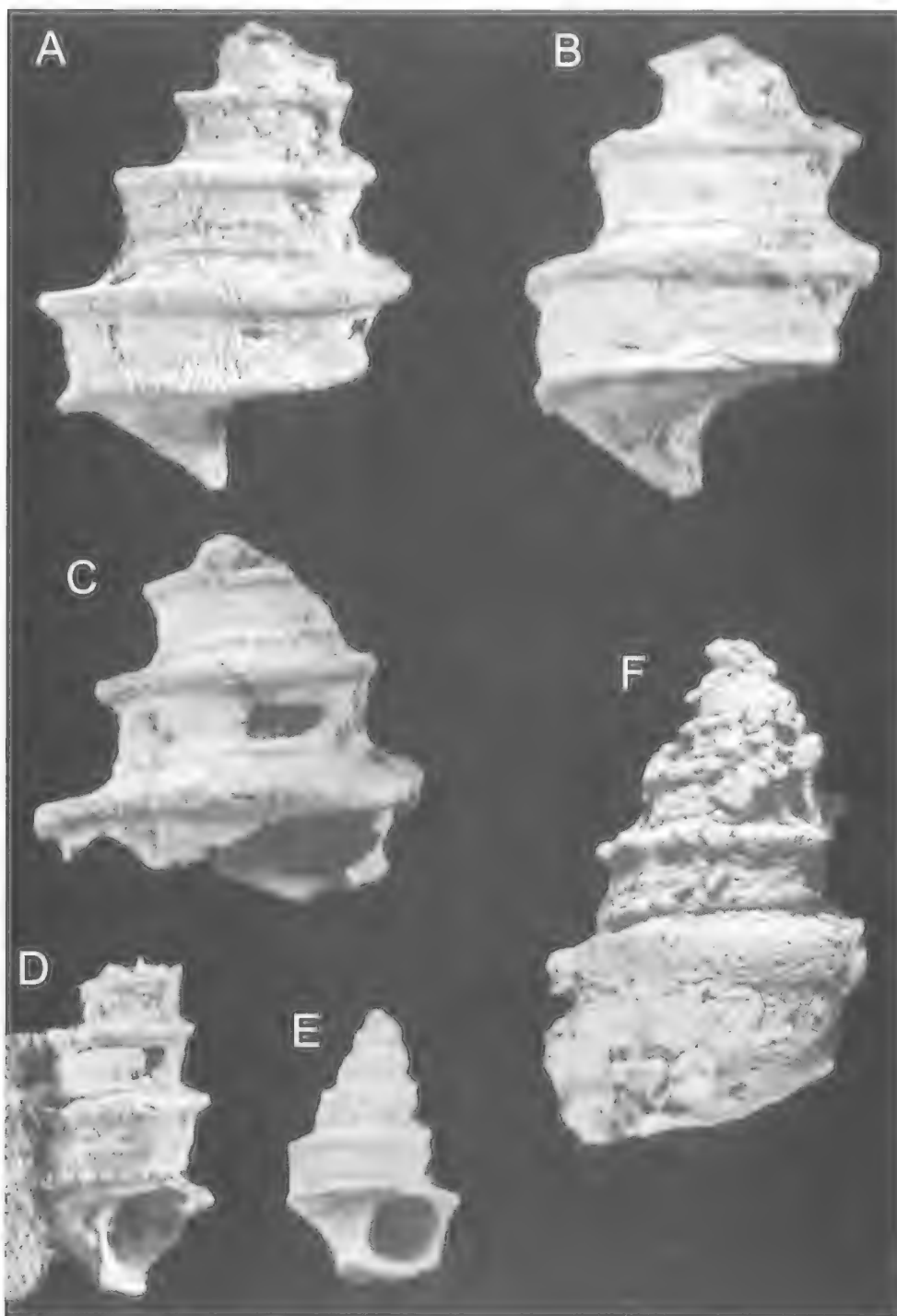


FIG. 3. A-F, *Cheeneetnukia frydai* gen. et sp. nov. A, Paratype E UAM 2644, $\times 2$, apertural view. B, Paratype F UAM 2645, $\times 2$, apertural view. C, Paratype G UAM 2646, $\times 2$, side view of shell fragment. D, Paratype H, UAM 2647, $\times 2$, apertural view. E, Paratype I, UAM 2648, $\times 3$, apertural view. F, UAM 2649, $\times 1.5$, side view of coarsely preserved silicified specimen. A-E from locality 79RB8 (USGS locality 10061-SD), McGrath A-5 quadrangle, west-central Alaska, F from USGS locality M1299-SD, Craig D-4 quadrangle, southeast Alaska.

columellar lip thin, arcuate, recurved; outer lip unknown; growth lines typically not preserved, but visible on a few upper whorl surfaces where they are weakly prosocline (nearly orthocline).

REMARKS. The largest complete specimen in the collection is the holotype with the following dimensions: height (incomplete), 58.0mm; width (incomplete), 40.0mm. As noted above, the depth of the umbilicus is variable, in adult specimens it is minutely phaneromphalous, but width is variable (compare Figs 1C and 2D), in juvenile specimens the base of the shell is typically cryptomphalous. The 'squared-off' (rectangular) whorl profile is clearly shown in Fig. 2B, C. Several specimens show a weak development of nodes along the flange-like carina that forms the upper angulation, weakly anticipating the more strongly nodose character of many Givetian members of the Cheeneetnukiidae.

COMPARISON. This species differs from *Cheeneetnukia australis* in having a more strongly developed and protruding flange-like upper angulation.

OCCURRENCE. This species is especially abundant and one of the most abundant at locality 79RB8 (>128 specimens) in the upper part (early Eifelian) of the Cheeneetnuk Limestone in the McGrath A-5 quadrangle, west-central Alaska (Nixon Fork subterrane of the Farewell terrane). The species is also present in lesser abundance in nearby, stratigraphically higher locality 79RB9. Both horizons are approximately 3 m thick and located along the type section traverse; the top of older horizon and the top of the younger horizon are 101m and 82m below the top of the Cheeneetnuk Limestone, respectively. Each locality is essentially the same on the 1:63,360 scale McGrath A-5 quadrangle map (Rigby & Blodgett, 1983, fig. 1; Blodgett & Rohr, 1989: fig. 2). The age of these two localities is probably late early to middle Eifelian, based on the co-occurrence and range overlap of the conodont *Polygnathus costatus costatus* (ident. N.M. Savage in Blodgett & Gilbert, 1983) and the ammonoid *Pinacites jugleri* (House & Blodgett, 1982). In addition, this new gastropod species is also recognised from Eifelian strata of the Wadleigh Limestone in the Craig D-4 quadrangle, SE Alaska (Alexander terrane). It is present there in a collection (field number 68Aes596; =USGS locality M1299-SD) made by J. Evans of the U.S. Geological Survey in 1988; specimens from there being coarsely

silicified. The locality is situated on the shoreline of a small islet in the NW¼, NE¼, section 34, T70S, R79E, Craig D-4 quadrangle.

***Cheeneetnukia australis* sp. nov.**
(Fig. 4A,B)

murchisonioid indet. Cook & Camilleri 1997: 71, fig. 4A-B.

TYPES. Holotype QMF33100 (Cook & Camilleri, 1997, fig. 4A); Paratypes QMF33097 and 34529 (Cook & Camilleri, 1997: fig. 4B), all from Queensland Museum Locality 1019.

ETYMOLOGY. Latin, *australis*, southern.

DIAGNOSIS. Upper angulation markedly reduced, weakly protruding.

DESCRIPTION. Medium-sized, moderately high-spired, turbiniiform gradate shell up to 28mm high and 20mm wide, with an apical angle of c. 30°. Upper whorl surface with prominent sutural ramp sloping very gently to peripheral rounded keel. Midwhorl surface wide and vertical, with selenizone bordered by 2 weak threads. Lower whorl face rounded, but poorly known in the material. Suture slightly impressed, situated at lower part of midwhorl surface. Base unknown. Collabral growth lines, fine, numerous, closely spaced, prosocline on sutural ramp and above selenizone, opisthocline below selenizone. [original description of Cook & Camilleri (1997: 71)].

COMPARISON. This species differs from the type species, *C. frydai*, primarily in having a less prominently protruding upper angulation and in having much stronger spiral threads bordering the selenizone.

OCCURRENCE. Represented by three specimens from the uppermost Dosey Limestone (early Givetian, *ensensis* - lower *varcus* CZ), Broken River Province, north Queensland. This species differs from *C. frydai* in having a much less protruding flange-like upper angulation, but nevertheless is congeneric in every other respect.

***Ulungaratoconcha* gen. nov.**

TYPE SPECIES. *Ulungaratoconcha heidelbergeri* gen. et sp. nov. from the Middle Devonian (Eifelian) strata of the Ulungar Formation (Anderson, 1991), Alaska.

ETYMOLOGY. *Ungularat*, for the Ulungar Formation and *concha* Latin for shell.

DIAGNOSIS. Narrowly acute, turbiniiform, high-spired shell with flat to gently inclined, relatively narrow ramp-like upper whorl face and

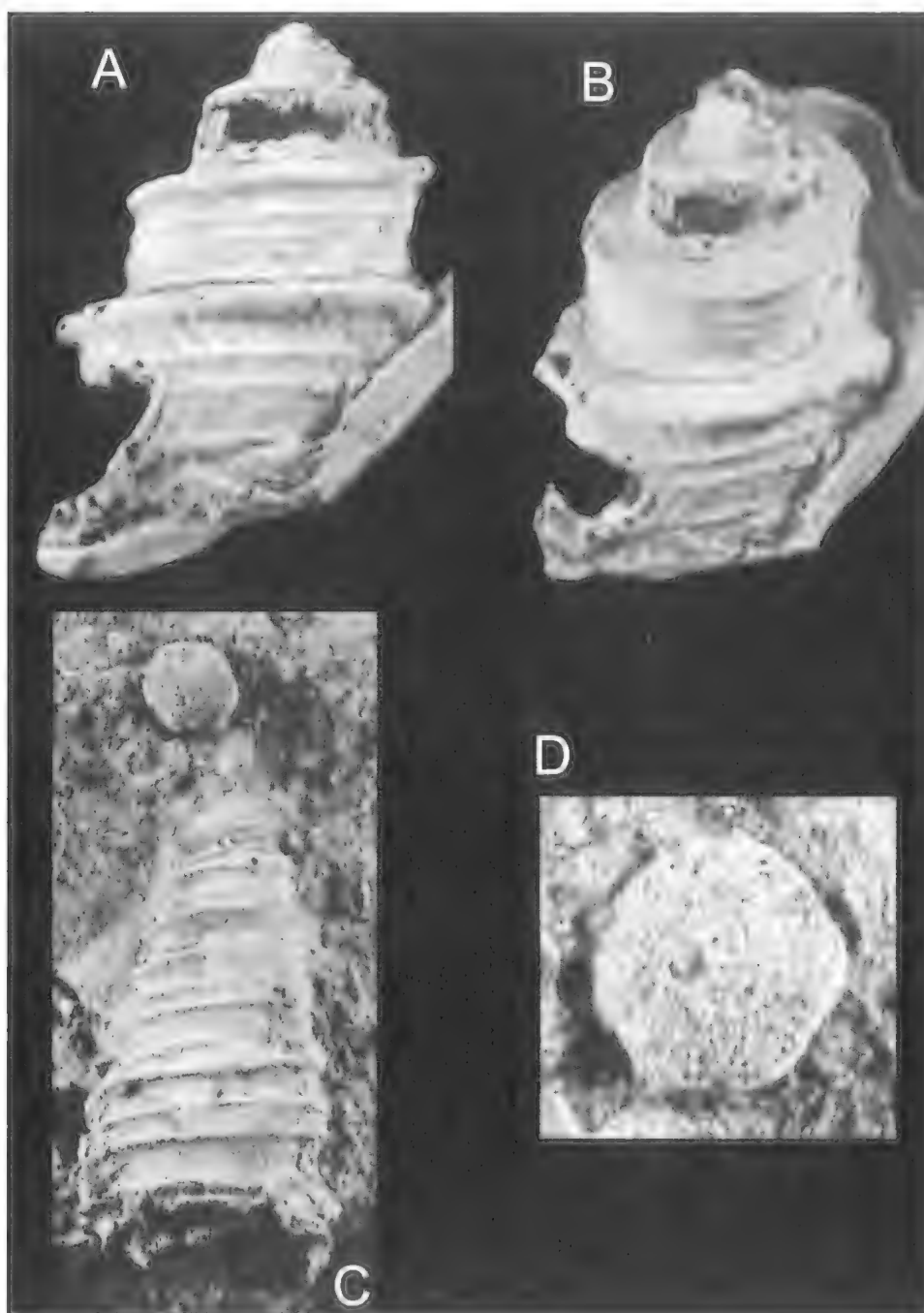


FIG. 4. A-B, *Cheeneetnukia australis* gen. et sp. nov. Latex replica of Holotype, QMF33100, $\times 2$. A, side view; B, oblique side view. C, *Ulungaratoconcha heidelbergeri* gen. et sp. nov. Latex replica of Holotype, UAM 2650, $\times 3$, side view. D, *Coelotrochium* sp., a calcareous green alga (same specimen above gastropod shown in C) commonly found in Eifelian age shallow-water gastropod-dominated communities in Alaska's accreted terranes (i.e. Farewell, Alexander, Livengood, and Arctic Alaska terranes), $\times 9$. A-B is from the uppermost Dosey Limestone (early Givetian), north Queensland, and C-D are from the Ulungarat Formation in the Demarcation D-4 quadrangle, northeast Brooks Range, northeast Alaska (North Slope subterrane of the Arctic Alaska terrane).

vertical outer whorl face with centrally situated selenizone; upper/outer angulation commonly produced into a strongly protruding flange-like ridge. Younger members (Givetian) may develop nodes or spines.

COMPARISON. *Ulungaratoconcha* gen. nov. shares the distinctive squared-off whorl profile and distinctive flange-like upper angulation also found in *Cheeneetnukia* gen. nov., but is easily distinguished from it by its narrowly acute spire, compared to the broad, gradate (step-like) shell form of the latter genus.

COMPOSITION. Species names are given after original author usage. Heidelberg (2001) provided excellent photographs of many of these species.

Ulungaratoconcha heidelbergi gen. et sp. nov. (type species); Eifelian of Alaska.

Murchisonia coronata D'Archiac & DeVerneuil, 1842; Givetian of Germany.

Murchisonia archiaci var. *intermediacoronata* Andree, 1928; Givetian of Germany.

Murchisonia bigranulosa D'Archiac & DeVerneuil, 1842; Givetian of Germany.

Murchisonia binodosa D'Archiac & DeVerneuil, 1842; Givetian of Germany.

Murchisonia intermedia D'Archiac & DeVerneuil, 1842; Givetian of Germany.

Murchisonia archiaci var. *coronaturbinata* Andree, 1928; Givetian of Germany.

Murchisonia archiaci var. nov. *bicoronata* PaECKELMANN, 1922; Givetian of Germany.

Murchisonia hibernia Heidelberg, 2001; Givetian of Germany.

Murchisonia pseudobinodosa Heidelberg, 2001; Givetian of Germany.

***Ulungaratoconcha heidelbergi* sp. nov.**
(Fig. 4C)

MATERIAL. Holotype, UAM 2650.

ETYMOLOGY. For Karlheinz Heidelberg, husband and ardent field assistant of German Devonian gastropod worker Doris Heidelberg.

DIAGNOSIS. Spire highly acute, narrow; lacking nodes or spines.

DESCRIPTION. Medium-sized (16.8mm (incomplete) high; 9.3mm wide), acutely high-spired (pleural angle about 12°), turbiniform shell; whorls up to at least five; sutures weakly incised, situated immediately beneath projecting edge of lower angulation; protoconch and initial portion of shell unknown; upper whorl face

formed by moderately inclined, narrow ramp, outer whorl face flattened, weakly convex, with relatively broad (occupying about 1/3 of whorl face), centrally located selenizone, the latter bordered by two strongly raised, sharp-edged spiral threads which project to form shell periphery, boundary between upper and outer whorl faces occupied by flange-like projecting upper angulation, lower boundary of outer whorl face formed by lower angulation which likewise bears a strongly projecting flange-like edge; growth lines prosocline (closely approaching orthocline) on upper whorl face, those on outer whorl face are evenly and more strongly inclined at approximately 60° from horizontal, being prosocline above and opisthocline below the selenizone; surface of selenizone flat, with no visible lunulae; base of shell unknown.

COMPARISON. This species, the oldest known representative of the genus, most closely resembles the Givetian *Murchisonia coronata* D'Archiac & DeVerneuil, 1842, and *M. intermediacoronata* Andree, 1928, but is distinguished from both in having a more narrowly acute spire. Its lack of nodes or spines distinguishes it from most of the other species provisionally placed in the genus.

OCCURRENCE. The single specimen was collected by Arlene V. Anderson (then a doctoral student at the University of Alaska Fairbanks). It is from the Ulungarat Formation (Anderson, 1991) exposed in the NE Brooks Range. The locality (field number 89A-126A₁) is within member A, the lowermost and only marine unit of the four members (Anderson, 1991, 1993). The collection which yielded this sample was derived from a 14m thick interval of chert arenite and siltstone with thin interbeds of mudstone that forms the base of her measured section 89A-118, situated at and just below the 6,000 foot contour elevation in the SW¼, NW¼, SE¼, section 16, T5S, R37E, Demarcation Point A-4 quadrangle (Anderson, 1993: 228). This interval comprises the lowermost in-place outcrop above a loose scree slope. This new gastropod species has previously been cited as representing a 'new genus of murchisoniid gastropod' (Popov et al., 1993: 1214; Blodgett et al., in press). The sandstone piece that yielded this specimen also contains the dasyclad alga *Coelotrochium* (Fig. 4D), a common floral associate in Eifelian gastropod-rich communities in various accreted Alaskan terranes (Farewell, Alexander, Livengood and Arctic Alaska).

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Grateful appreciation is due Wyatt G. Gilbert, whose 1979 summer field mapping program in the McGrath A-4 and A-5 quadrangles, made possible the collection of the Cheeneetnuk Limestone specimens. Arlene V. Anderson kindly allowed examination of her doctoral dissertation collection from the Demarcation Point quadrangle, eastern Brooks Range of Alaska. RBB thanks the Alexander von Humboldt Stiftung for providing financial support that allowed him a six month stay in Germany to study European Devonian gastropods. AGC thanks Peter Jell and the Trustees of the Queensland Museum for support enabling travel to North America during 1997. We also wish to thank A.J. Boucot, Jiri Frýda, and Alex Nützel for their thoughtful reviews of this manuscript.

LITERATURE CITED

- ANDERSON, A.V. 1991. Ulunguat Formation type section of a new formation, headwaters of the Kongakut River, eastern Brooks Range, Alaska. Alaska Division of Geological and Geophysical Surveys, Public Data File 91-4.
1993. Stratigraphic variation across a Middle Devonian to Mississippian rift-basin margin and implications for subsequent fold and thrust geometry, northeastern Brooks Range, Alaska. Unpubl. PhD dissertation, University of Alaska, Fairbanks, Alaska.
- ANDRÉ, J. 1928. Über mitteldevonische Murchisonien. *Palaeontologische Zeitschrift* 9: 357-366.
- ARCHIAC, E.J.A. D' & DeVERNEUIL, E.P. 1842. On the fossils of the older deposits in the Rhenish provinces, preceded by a general survey of the fauna of Palaeozoic rocks, and followed by a tabular list of the organic remains of the Devonian System in Europe. *Transactions of the Geological Society of London* 6: 303-410.
- BLODGETT, R.B. 1997. Emsian (Late Early Devonian) fossils indicate a Siberian origin for the Farewell terrane. *Short Notes on Alaskan Geology* 1997. Alaska Division of Geological and Geophysical Surveys Professional Report 118: 27-34.
- BLODGETT, R.B. & BOUCOT, A.J. 1999. Late Early Devonian (late Emsian) coelospiriferinid brachiopods from Shellabarger Pass, Talkeetna C-6 quadrangle, south-central Alaska and their biogeographic importance; further evidence for a Siberian origin of the Farewell and allied Alaskan accreted terranes. *Senckenbergiana lethaea* 72(1): 209-221.
- BLODGETT, R.B. & BRILASE, P.F. 1997. Emsian (late Early Devonian) brachiopods from Shellabarger Pass, Talkeetna C-6 quadrangle, Denali National Park, Alaska indicate Siberian origin for Farewell terrane. *Geological Society of America, Abstracts with Programs* 29(5): 5.
- BLODGETT, R.B. & GILBERT, W.G. 1983. The Cheeneetnuk Limestone, a new Early(?) to Middle Devonian formation in the McGrath A-4 and A-5 quadrangles, west-central Alaska. *Alaska Geological & Geophysical Surveys Professional Report* 85.
- BLODGETT, R.B. & ROHR, D.M. 1989. Two new Devonian spine-bearing pleurotomaricean gastropod genera from Alaska. *Journal of Paleontology* 63: 47-53.
- BLODGETT, R.B., ROHR, D.M. & BOUCOT, A.J. 1989. Early and Middle Devonian gastropod biogeography. Pp. 277-284. In: McKenrow, W.S. & Scolese, C.R. (eds) *Palaeozoic palaeogeography and biogeography*, Memoir 12. (Geological Society: London).
- In press. Paleozoic linkages among some Alaskan accreted terranes and Siberia based on megafossils. In: Miller, E.J., Grantz, A., & Klempner, S. (eds) *Tectonic evolution of the Bering Shelf-Chukchi Sea-Arctic Margin and adjacent landmasses*. *Geological Society of America Special Paper* 360.
- COOK, A.G. & CAMILLERI, N. 1997. Middle Devonian gastropods from the Broken River Province, north Queensland. *Memoirs of the Queensland Museum* 42: 55-79.
- COX, L.R. & KNIGHT, J.B. 1960. Suborders of Archaeogastropoda. *Proceedings of the Malacological Society of London* 33: 262-264.
- DECHEN, E.H.C. von, 1832, in De la BÉCHE, H.T. *Handbuch der Geognosie*, 533-534. Berlin.
- FRÝDA, J. 1999a. Higher classification of the Paleozoic gastropods inferred from their early shell ontogeny. *Journal of the Czech Geological Society* 44: 137-153.
- 1999b. Shape convergence in gastropod shells: an example from the Early Devonian Plectonotus (Boucotonotus) - Palaeozygopleura Community of the Prague Basin (Bohemia). *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 83: 179-190.
2001. Discovery of a larval shell in Middle Paleozoic subulitoidean gastropods with description of two new species from the Early Devonian of Bohemia. *Bulletin of the Czech Geological Survey* 76(1): 29-37.
- FRÝDA, J. & BLODGETT, R.B. 2001. The oldest known heterobranch gastropod, *Kuskokwimia* gen. nov., from the Early Devonian of west-central Alaska, with notes on the early phylogeny of higher gastropods. *Bulletin of the Czech Geological Survey* 76(1): 39-53.
- FRÝDA, J. & MANDA, S. 1997. A gastropod faunule from the Monograptus uniformis graptolite Biozone (Early Lochkovian, Early Devonian) in Bohemia. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 80: 59-122.

- GARCIA-ALCALDE, J. & BLODGETT, R.B. 2001. New Lower Devonian (Upper Emsian) *Myriospirifer* (Brachiopoda, Eospiriferinae) species from Alaska and northern Spain and the paleogeographic distribution of the genus *Myriospirifer*. *Journal of the Czech Geological Society*, Havlíček volume 46(3/4): 59-68.
- GOLDFUSS, A. 1841-1844. *Petrefacta Germaniae*. (Dritter Theil: Düsseldorf).
- GRÜNEBERG, H. 1927. Vererbungswissenschaftliche Studien über einige Murchisonien des oberen Mitteldevons. *Zeitschrift der Deutschen Geologische Gesellschaft* 1927: 383-404.
- HEIDELBERGER, D. 2001. Mitteldevonische (Givetische) Gastropoden (Mollusca) aus der Lahnmulde (südliches Rheinisches Schiefergebirge). *Geologische Abhandlungen Hessen* 106: 1-291.
- HOUSE, M.R. & BLODGETT, R.B. 1982. The Devonian goniatite genera *Pinacites* and *Foordites* from Alaska. *Canadian Journal of Earth Science* 19: 1873-1876.
- JELL, J.S., SIMPSON, A., MAWSON, R. & TALENT, J.A. 1993. Biostratigraphic summary. In: Withnall, I.W. & Lang, S.C. (eds) *Geology of the Broken River Province, north Queensland*. *Queensland Geology* 4: 239-245.
- KNIGHT, J.B., COX, L. R., KEEN, A.M., BATTEN, R.L., YOCHELSON, E.L. & ROBERTSON, R. 1960. Systematic descriptions. Pp. 1169-1324. In: Moore R.C. (ed.) *Treatise on invertebrate paleontology, Part I, Mollusca 1*. (Geological Society of America and University of Kansas Press: Lawrence).
- KIRCHNER, H.S. 1915. Mitteldevonische Gastropoden von Soetenich in der Eifel. *Verhandlungen des Naturhistorischen Verreins der preussischen Rheinlande und Westfalens* 71: 189-261.
- KOKEN, E. 1896. *Die Leitfossilien*. (Chr. Herm. Tauchnitz: Leipzig).
- LOTZ, H. 1900. Die Fauna des Massenkalks der Lindener Mark bei Giessen. *Schriften der Gesellschaft zur Beförderung der gesamten Naturwissenschaften zu Marburg* 13.
- MANSUY, H. 1912. *Étude géologique du Yun-nan oriental, 2^e partie, Paléontologie*. *Mémoires du Service géologique de l'Indo-Chine* 1(2).
- METCALFE, I. 1996. Gondwanaland dispersion, Asian accretion and evolution of eastern Tethys. *Australian Journal of Earth Sciences* 43: 605-623.
- NÜTZEL, A. & BANDEL, K. 2000. Goniasmidae and Orthonemidae: two new families of the Palaeozoic Caenogastropoda (Mollusca, Gastropoda). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 9: 557-569.
- PAECKELMANN, W. 1922. Der mitteldevonische Massenkalk des Bergischen Landes. *Abhandlungen der Preussischen Geologischen Landesanstalt, Neue Folge* 91.
- PHILLIPS, J. 1841. Figures and descriptions of the Palaeozoic fossils of Cornwall, Devon, and West Somerset; observed in the course of the ordnance geological survey of that district. (Brown, Green, & Longmans: London).
- POPOV, L.Y., BLODGETT, R.B. & ANDERSON, A.V. 1994. First occurrence of the genus *Bicarinatina* (Brachiopoda, Inarticulata) from the Middle Devonian in North America (Alaska). *Journal of Paleontology* 68: 1214-1218.
- RIGBY, J.K. & BLODGETT, R.B. 1983. Early Middle Devonian sponges from the McGrath quadrangle of west-central Alaska. *Journal of Paleontology* 57: 773-786.
- SANDBERGER, G. & SANDBERGER, F. 1850-1856. *Die Versteinerungen des Rheinischen Schichtensystems in Nassau*. (Kreidel und Neidner: Wiesbaden).
- SCOTese, C.R. & McKERROW, W.S. 1989. Revised World maps and introduction. In: McKerrow, W.S. & Scotese, C.R. (eds) *Palaeozoic palaeogeography and biogeography*. Geological Society (London) *Memoir* 12: 1-21.
- SUNTHARALINGAM, T. 1968. Upper Palaeozoic stratigraphy of the area west of Kampar, Perak. *Geological Society of Malayasia, Bulletin* 1: 1-15.
- TASSELL, C.B. 1980. Further gastropods from the Early Devonian Lilydale Limestone, Victoria. *Records of the Queen Victoria Museum, Launceston* 69: 1-27.
- WHIDBORNE, G.F. 1889-1892. A monograph of the Devonian fauna of the South of England, Vol. 1, The fauna of the limestones of Lummaton, Wolborough, Chircombe Bridge, and Chudleigh. *Palaeontographical Society, London*.
- WHITEAVES, J.F. 1892. The fossils of the Devonian rocks of the islands, shores or immediate vicinity of Lakes Manitoba and Winnipegosis. *Contributions to Canadian Palaeontology* 1(4): 255-359.
- WINTERFELD, F. 1894. Ueber den mitteldevonischen Kalk von Paffrath. *Zeitschrift der Deutschen Geologischen Gesellschaft* 46: 687-696.



FIVE NEW GENERA OF FREE-LIVING MARINE NEMATODES FROM SANDY BEACHES OF EASTERN AUSTRALIA

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Five new genera of free-living marine nematodes are described from exposed sandy beaches on the eastern coasts of Queensland and New South Wales. *Macquaria chimaira* gen. et sp. nov. (Chromadoridae), is distinguishable from other Euchromadorinae by the armature of the buccal cavity, the conspicuous posterior oesophageal bulb, and pre- and postcloacal ventromedian cuticular thickenings in the male. *Onchiolistia multipapillata* gen. et sp. nov. (Leptolaimidae) has an onchiostyle plus alveolar and tubular ventromedian supplements in the male thus separating it from other Camacolaiminae. *Procamacolaimus tubifer* Gerlach and Furstenberg & Vincx and *P. africanus* Furstenberg & Vincx are transferred to the new genus. The xyalid *Pseudechinotheristus nudus* gen. et sp. nov. is very closely related to *Echinotheristus* Thun & Riemann but distinguishable by the absence of the typical cuticular spines and the bladder-like supplements in male. *Dactylaimoides coronifer* gen. et sp. nov. differs mainly from other xyalid genera by the coarse, complicated cuticle with longitudinal crests with a point of reversal and the conspicuous light refractive crown-like ring in the anterior buccal cavity. *Paragonionchus sclerolabius* gen. et sp. nov. is set off from other xyalid genera by the coarse cuticle with longitudinal crests, the deeply incised lips with peculiar cuticularised supporting structures, and the arrangement of the cephalic sensillae. □ *Nematoda, eastern Australia, sandy beaches, taxonomy.*

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This paper erects five new nematode genera based on material collected from exposed sandy beaches along the Australian east coast in 1997 and 1998 during investigations on latitudinal gradients in biodiversity of selected meiobenthic taxa (Free-living Platyhelminthes, Gastrotricha, and Free-living Nematoda).

MATERIALS AND METHODS

Collections considered here were made in Queensland on a beach next to the village of Thursday Island, on Forrest Beach at Innisfail, and on Alva Beach at Ayr, and in New South Wales on Ocean View Beach at Arrawarra, and on Shelly Beach at Port Macquarie.

Samples were taken in the intertidal zone at low water by pushing cylindrical perspex corers (2.4cm internal diameter and 5.0cm long) into the sand. Nematodes were extracted using the SMB-method (Noldt & Wehrenberg, 1984), fixed in 4% formaldehyde in tap water and processed to permanent glycerol mounts (Blome, 1983). Type material is deposited in the Queensland Museum, Brisbane.

ABBREVIATIONS. L=body length; a=L divided by maximum body diameter; b=L divided by oesophageal length; c=L divided by tail length; c.d.= corresponding diameter; h.d.=head diameter; juv.=juvenile(s); ♂=male; ♀=female; g♀=gravid female; R₁₋₃=rings of cephalic setation; V=distance of vulva from head in % of L; i.a.=inter alia (among other things)

SYSTEMATICS

CHROMADORIDA Filipjev, 1929
CHROMADORINA Filipjev, 1929
CHROMADORIDAE Filipjev, 1917
EUCHROMADORINAE Gerlach & Riemann, 1973

Macquaria gen. nov.

DIAGNOSIS. Euchromadorinae. Cuticle complex with lateral differentiation formed by two longitudinal rows of enlarged dots joined by transverse bars. Amphids transverse slits without marked thickening of the margins. Cephalic sensillae in three separate rings, whereas the sensillae of the first ring are papilliform and the four setae of R₃ longer than that ones of R₂. Solid

dorsal tooth opposed by two small ventral teeth, all with flanges forming a cylindrical posterior part of buccal cavity. Oesophagus with well developed posterior bulb. Males with single outstretched anterior testis, right of the intestine. ♀ with opposed, reflexed ovaries, the anterior one right, the posterior one left of intestine. Spicular apparatus consisting of weakly cuticularised, arcuate spicules, a gubernaculum of irregular shape, and lateral pieces of indistinctly L-shaped form. Ventrally pre- and postloaeal cuticular thickenings in ♂♂. Tail conical with three indistinct caudal glands.

TYPE SPECIES: *Macquaria chimaira* sp. nov.

ETYMOLOGY. From Port Macquarie, NSW.

DISCUSSION. Members of Euchromadorinae are mainly characterized by complex cuticle, often with lateral differentiation and with a point of reversal in the pattern; buccal cavity mostly with solid dorsal tooth and often with series of denticles; amphids transverse slits or oval openings with double contour; oesophagus mostly without definite posterior bulb; most genera with hammer- or L-shaped lateral pieces; preloaeal structures or supplements usually absent.

The Euchromadorinae is widely regarded as containing 10 genera (Warwick & Coles, 1975; Platt & Warwick, 1988), to be supplemented by *Crestanema* Pastor de Ward, 1985.

Two of those genera do not have lateral pieces (*Endeolophos* Boucher, 1976; *Trochamus* Boucher & Boyée, 1972), and *Dicricanema* Steiner & Hoeppli, 1926 is known from a female, only. *Actinonema* Cobb, 1920 and *Rhipx* Cobb, 1920 are both characterized by amphids with double contours and by double-jointed spicules in the latter genus. *Parapinnanema* Inglis, 1969, *Nygmatonchus* Cobb, 1933 and *Crestanema* have 10 (6+4) cephalic setae in one ring, departing from the usual pattern in this respect.

Euchromadora de Man, 1886 is distinguished from *Macquaria* in having denticles and by lacking a lateral cuticular differentiation, a posterior oesophageal bulb, and pre- or postloaeal structures.

In *Graphonema* Cobb, 1898 the dorsal tooth appears hollow (Platt & Warwick, 1988), and there is no posterior oesophageal bulb, no preloaeal differentiation, and no lateral differentiation of the cuticle.

Parapinnanema is similar to *Graphonema* but

differs from the latter in having prominent preloaeal structures in the male, and shares this character with *Macquaria*.

Steineridora Inglis, 1969 has a massive squarish dorsal tooth, denticles and a posterior oesophageal bulb, but shows neither a preloaeal differentiation nor a lateral differentiation of cuticle.

According to Pastor de Ward (1985), *Crestanema* shows 6+4 cephalic setae in one ring, oval amphids with simple contour and a lateral differentiation of cuticle different in structure from that in *Macquaria*.

Macquaria is characterized by a unique combination of Euchromadorinae characters: the dorsal tooth is obviously solid in its basal part and in the dorsal shoulder, and there are flanges on the lateral walls of oesophastome as well as ventral onchia (cf. *Graphonema*). The cuticle in the anterior part of the oesophagus is more thickened (cf. *Parapinnanema*) and the oesophagus has a conspicuous posterior bulb (cf. *Steineridora*).

The amphids are faint, without surrounding fringe of cuticle, and there is a distinct lateral differentiation of the cuticle from the anterior end to the tail-tip.

Macquaria chimaira sp. nov.

(Fig. 1)

MATERIAL EXAMINED. HOLOTYPE, QMG218930, ♂, Port Macquarie, Shelly Beach, 03.09.1997, embedded in glycerol. D. Blome. PARATYPES, QMG218931, ♂, same data as holotype, and QMG218932, ♀, Arrawarra, Ocean View Beach, 25.08.1997. D. Blome. OTHER MATERIAL. ♀, ♀, 1 juv. - Port Macquarie, Shelly Beach; 3♂, 3♀ - Arrawarra, Ocean View Beach. D. Blome.

ETYMOLOGY. Greek *chimaira*, monstrosity composed from parts of a lion, goat, and snake (Greek mythology) - referring to the mixture of characters of Euchromadorinae combined in this new genus.

MORPHOMETRIC DATA. ♂ (holotype): L = 1019 µm; a = 35.1; b = 7.5; c = 7.8; Spicules 30 µm on the chord. ♂: L = 1024 µm; a = 37.9; b = 7.8; c = 8.0; Spicules 27 µm on the chord. ♀: L = 872 µm; a = 30.3; b = 7.5; c = 8.7; V = 54%.

DESCRIPTION. Relatively slender, gradually tapering from neck region towards head.

Males (mainly referring to holotype): Cuticle complex; in neck region, especially anterior to nerve ring, relatively coarsely punctated, thick. Posterior to head annules first are finely dotted, from the second pair of ring pores the coarser dots fuse into notched annules all over the total body

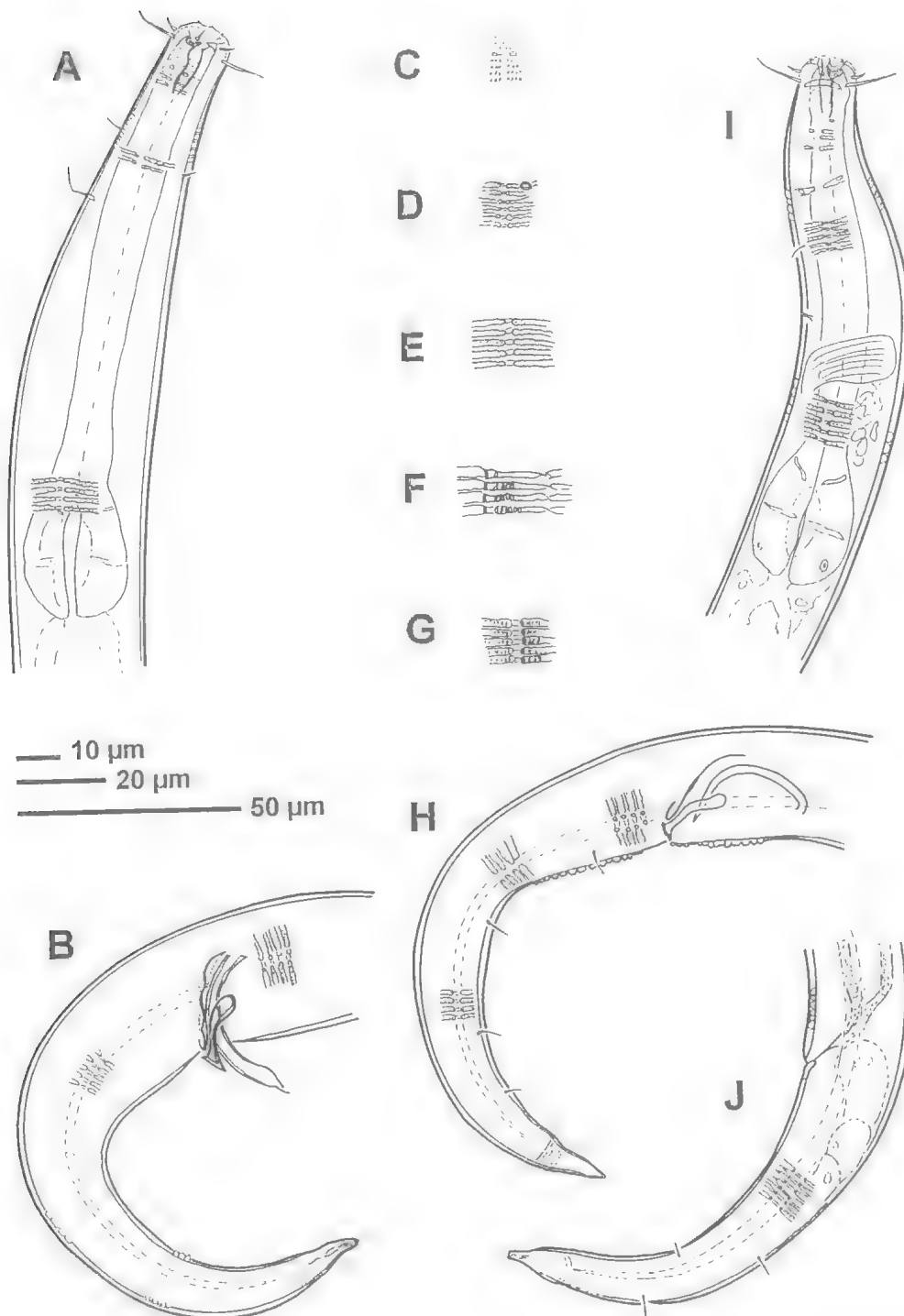


FIG. 1. *Macquaria chimaira* gen. et sp. nov. A-G, ♂, holotype: A, head; B, tail region and spicular apparatus; C, cuticular structure behind head (from 1. ring); D, at neck region (18. ring and posterior); E, at end of oesophagus; F, at middle of body-length; G, at cloacal region. H, ♀, paratype 2: tail region. I-J, gravid ♀, paratype: I, head; J, tail region.

length. A lateral differentiation of two longitudinal rows of larger dots ($1.6\mu\text{m}$ apart at head, $2.4\mu\text{m}$ at cardia and anus, and 3.2 in middle of the body), joined by transverse bars, runs from the head to the spinneret. Those enlarged dots are flanked by transverse rows of finer punctations. Amphids transverse slits, $4.8\mu\text{m}$ posterior to front end (i.e. more or less at level of R_3), $8.0\mu\text{m}$ wide (62% of c.d.) and $1.6\mu\text{m}$ in length. Cephalic setae in 3 separated rings: R_1 papilliform, R_2 6 setae of $4\mu\text{m}$ length, R_3 4 $12\mu\text{m}$ long setae. Dorsal tooth medium sized, solid, slightly sickle-shaped, with flange of $12\mu\text{m}$ length; opposed by two tiny ventral teeth with flange of $11\mu\text{m}$, curved. Buccal cavity in total $16\text{--}17\mu\text{m}$ long and in its posterior (cylindrical) part $2.4\mu\text{m}$ wide. Oesophagus with prominent posterior bulb measuring $31\times 24\mu\text{m}$. Ventral gland not seen; an exit pore is located at $62\mu\text{m}$ posterior to anterior end in δ_1 and at $68\mu\text{m}$ in δ_2 . The single, outstretched, anterior testis is situated to the right of the intestine. Details of the male gonad, especially of the vas deferens, not visible. Spicules slender, arcuate, weakly cuticularised, non-alate; distally with a nailform tip. Gubernaculum close to the spicules, of irregular shape; proximally curved and acute, distally rounded, blunt, measuring $24\mu\text{m}$ in δ_1 and $22\mu\text{m}$ in δ_2 . Lateral pieces simple, indistinctly L-shaped, $16\mu\text{m}$ long; proximal end well rounded, distally slightly widened and with sharp edges. Anterior to the cloaca the ventral body cuticle (with coarser annulation) is thickened into a distinctively raised area of about $20\mu\text{m}$ length. Postcloacally the same holds for a distance of about $25\mu\text{m}$. Tail conical, $4.5\text{--}5.1$ of anal body diameter long. Three indistinct caudal glands. Four pairs of subventral setae.

Female (paratype): Resembling the male in general appearance. Exit of the ventral gland at $56\mu\text{m}$ posterior to the anterior end. Ovaries opposed, reflexed; anterior one right, posterior one left of intestine. Tip of anterior ovary $90\mu\text{m}$ anterior to vulva, reflexion at $236\mu\text{m}$ anterior to vulva. Tip of posterior ovary $108\mu\text{m}$ posterior to vulva, reflexion $228\mu\text{m}$ posterior to vulva. Vagina wide, well cuticularised respectively muscular. Uteri as spermathecae, filled with voluminous, round to oblong sperm cells.

DIAGNOSIS. As for genus

LEPTOLAIMINA Lorenzen, 1981
LEPTOLAIMIDAE Örley, 1880
CAMACOLAIMINAE Micoletzky, 1924

Onchiolistia gen. nov.

DIAGNOSIS. Cuticle thick, coarsely annulated; annules bearing faint longitudinal striae. Amphids ventrally wound modified spirals with circular to oblong apertures, situated at level of the cephalic setae (R_3). Buccal cavity nearly cylindrical with a solid onchiostyle in the dorsal wall, which possibly may be protrusible (Fig. 2C). Oesophagus indistinct, embedded in glandular tissue, at its posterior end being slightly clavate. Due to the position of the only male on the slide and its state of preservation no details of the male gonad visible. Female gonad monodelphic with one reflexed posterior ovary left of intestine. In male alveolar ventromedian supplements from the head end to nearly the mid of total body length plus tubular ventromedian supplements, present in precloacal position. Proximal ends (capitula) of spicules sharply bent ventrad. Tail uniformly conical with acute tip (spinneret), three caudal glands. Male tail with one indistinct ventromedian sensilla.

TYPE SPECIES. *Onchiolistia multipapillata* sp. n.

OTHER SPECIES. *Onchiolistia tubifera* (Gerlach, 1953), syn. *Procamacolaimus tubifer* Gerlach, 1953 sensu Gerlach (1953, 1962) and Furstenberg & Vincx (1988) comb. nov.; *Onchiolistia africana* (Furstenberg & Vincx, 1988), syn. *Procamacolaimus africanus* Furstenberg & Vincx, 1988 comb. nov..

ETYMOLOGY. With an onchiostyle in the dorsal wall of buccal cavity and closely related to *Listia* Blome, 1982.

DISCUSSION. Hope & Tchesunov (1999) revised the Camacolaiminae, gave a generic key and, among other taxonomic changes, synonymized *Eontolaimus* Furstenberg & Vincx, 1988 with *Listia*, transferring the latter into the Camacolaiminae. *Onchiolistia* is now added to the family. *Onchiolistia* resembles *Listia* apart from its onchiostyle.

The combination of such characters (onchiostyle+alveolar and tubular, ventromedian supplements in male) is only known from the descriptions of *Procamacolaimus tubifer* Gerlach, 1953 from Madagascar, later redescribed from the Maldives Islands (Gerlach, 1962) and a South African sandy beach (Furstenberg & Vincx, 1988).

Following the original diagnosis of *Procamacolaimus* (type-species: *P. acer* Gerlach, 1954)

the author did not mention nor depict alveolar, ventromedian supplements. Gerlach (1962:103) and Gerlach & Riemann (1973:47) noted that *Procamacolaimus* sensu Gerlach (1953a:82) and Gerlach (1953b: 602) are invalid names. Hence *P. tubifer* Gerlach, 1953 from Madagascar and *P. tubifer* Gerlach, 1962 from the Maldive Islands as well as the redescription of the species by Furstenberg & Vinex (1988) do not belong to this genus – nor does *P. africanus* Furstenberg & Vinex, 1988. Both species have to be transferred to the new genus because of the onchiostyle + alveolar and tubular ventromedian supplements in males.

***Onchiolistia multipapillata* sp. nov. (fig. 2)**

MATERIAL EXAMINED. HOLOTYPE, QMG218933, ♂, Thursday Island, beach south of the village, 12.10.1997, embedded in glycerol. D. Blome. PARATYPES, QMG218934, ♀₁ and QMG218935, ♀₂, same data as holotype. **OTHER MATERIAL:** ♀, 1 juv.; same data as holotype.

ETYMOLOGY. Latin *multus*, many, numerous; *papillatus*, provided with papillae.

MORPHOMETRIC DATA. ♂ (holotype): L = 1744 µm; a = 49.8; b = 6.9; c = 16.8; Spicules 44 µm on the chord. ♀₁: L = 1352 µm; a = 35.6; b = 6.0; c = 11.3; V = 43%. ♀₂: L = 1216 µm; a = 32.9; b = 5.4; c = 13.5; V = 45%.

DESCRIPTION. Body long, slender, nearly constant in width but significantly tapering towards the extremities. Anterior end measuring about 30% of the maximum body diameter, tail near tip also.

Male (holotype): Cuticle thick (1.6 µm), coarsely annulated. Annules 2.4 µm wide, with faint longitudinal striae. Body setation lacking, apart from 8–9 short (2.4 µm) scattered papillae in the neck region and 4 pairs of mostly subventral setose papillae on the tail. Hypodermal glands not seen. Amphids at level of the 4 cephalic setae, about 2.5 µm posterior to front end. They are ventrally wound and the apertures have a circular to oblong spiral contour (open posteriorly) of 6.4 µm length and 3.2 µm width (33% of c.d.). Sensillae of R₁ and R₂ not seen. Four cephalic setae (R₃) of 14 µm length (1.5 of c.d.). Buccal cavity approximately cylindrical (8.8x4.0 µm) with a solid 8.8 µm long onchiostyle in the dorsal wall. At least the anterior end of the onchiostyle is free from the surrounding tissue, the basal part of it is connected with the oesophageal tissue. The oesophageal musculature is indistinct, details of the cardia not visible. The intestinal tissue is also indifferent.

Ventral gland or its exit pore not seen. Due to the position (the body is twisted) and the state of preservation of the male no details of the gonad are visible. Spicular apparatus – visible only in dorsal view. Capitula and distal ends of the spicules ventrally directed. Distal ends appear thickened due to the close gubernacula. All structures delicately cuticularised and of irregular contour. There are 6 precloacal tubular supplements of 16 µm length, arranged at approximately regular distances (22–34 µm, mean = 27 µm), anteriormost one 160 µm, posteriormost 34 µm precloacal. A ventromedian row of 93 alveolar sensilla begins 35 µm behind the head and ends at 848 µm distance (= 47% of the body length). The alveoli mostly are equal-spaced, but some are arranged irregularly. Tail conical, 3.5 of cloacal body diameter long, tip pointed. Caudal glands inconspicuous. Four pairs of subventral setose papillae. An indistinct ventromedian papilla-like structure is situated at about 60% of the tail length.

Female (paratypes): General body shape similar to the male. Cuticle naked apart from three pairs of inconspicuous setose papillae (5 µm) in the neck region, whereas one pair is situated in front of a ventral pore and one pair behind it. One pair of postanal setose papillae of 4 µm length. Shape of the amphids as in male, obviously more circular, 5 µm long and 4 µm wide (56% of c.d.). Four cephalic setae measuring 13 µm, which equals 1.9–2.2 of head width. Buccal cavity 6 µm in length and 3 µm in width, onchiostyle measuring 7 µm. In ♀₁ the onchiostyle appears to be protrusible (fig. 2C). A ventral pore opens at 59% of oesophageal length (132 µm behind anterior end). Ventral gland not seen, due to the diffuse and glandular tissue surrounding the oesophagus. About 28 µm behind that ventral pore in ♀₂ the oesophagus widens slightly from 9 to 12–16 µm, forming a slender longish bulb comparable to that seen in plectids or dorylaimids. This posterior part of the oesophagus appears glandular, diffuse. The area around the ventral pore is filled with large, globular, glandular cells. Gonad monodelphic with one posteriorly reflexed ovary. A prevulvar spermatheca extending about 110 µm to the anterior in ♀₁, containing several big, globular sperm cells. In ♀₂ the ovary has a total length of 336 µm, the reflexion is situated 208 µm behind the vulva (i.e. 750 µm behind anterior end), the ovary tip is located 80 µm posterior to vulva (i.e. 622 µm behind anterior end). The total gonad is situated at the left of the intestine. Vulva

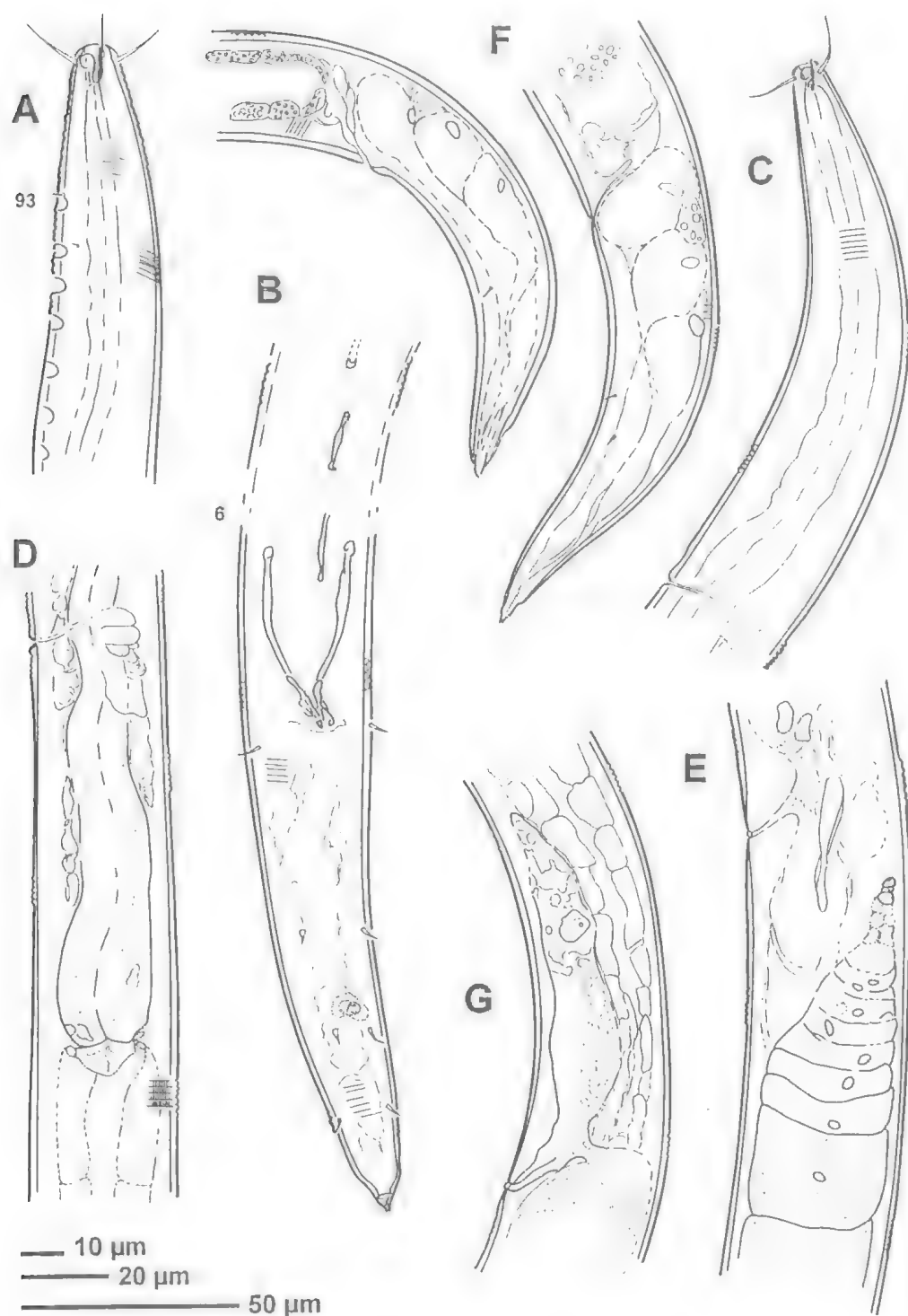


FIG. 2. *Onchiolistia multipapillata* gen. et sp. nov. A-B, ♂, holotype: A, head; B, tail region and spicular apparatus. C-F, gravid ♀, paratype 1: C, head; D, end of oesophagus; E, posterior part of ♀ gonadal tract (ovary); F, tail region. G-H, gravid ♀, paratype 2: G, anterior part of ♀ gonadal tract (spermatheca); H, tail region.

premedian (43-35%), vagina being a narrow duct of 12 µm length, directed anteriorly, with a weakly light refractive inner lining, altogether indistinct. Mature egg: 90x29 µm. Tail conical, spinneret well sclerotized, about 6-7 µm long, which equals the non-annulated terminal end. Three caudal glands. One pair of setose papillae (3 µm) at about half the length of tail.

REMARKS. *Onchololista multipapillata* sp. nov. is distinguished from the two congeneric species *O. africana* and *O. tubifera* generally by its larger body dimensions, length of cephalic setae (R_3) and length of spicules. Further the number of alveolar supplements in the male is about double that in the congeneric species, and finally, the size of male amphids in the new species is considerably less (33%) than in the other two species (40-50% in *O. tubifera* and 80% in *O. africana*).

MONHYSTERIDA Filipjev, 1929
MONHYSTEROIDEA de Man, 1876
XYALIDAE Chitwood, 1951

***Pseudechinotheristus* gen. nov.**

DIAGNOSIS. Cuticle coarsely annulated; annules bearing faint longitudinal striae. Amphids inconspicuous, transversely oval, showing sexual dimorphism in shape and size. Cephalic sensillae in two separate rings of the typical 6 + (6+4) pattern. Buccal cavity conical, with prominent ring in anterior part and funnel-shaped transition to oesophagus. Cardia small, glandular. Progaster with ciliary insecam. Ventral gland not seen. Testes opposed, outstretched, anterior one to the left, posterior one to the right of intestine. Spicules slightly asymmetrical in length, well cuticularized; proximally with a ring-like bulge, distally bifid. Lateral pieces well cuticularised of complicated form, distally bifid. No precloacal supplements. Female gonad monodelphic with an outstretched ovary left of intestine. Tail conical, plump. Two large caudal glands opening into two separate conical outlets.

TYPE SPECIES. *Pseudechinotheristus nudus* sp. nov.

ETYMOLOGY. Greek *pseudes*, remarkably like - similar to *Echinotheristus*

DISCUSSION: The new genus is very close to *Echinotheristus* sharing several peculiar characters with the latter as: general body shape, similarities in the head region (setation, ring in the buccal cavity, shape of buccal cavity), the

shape of amphids, and details in the male or female gonadal tract, respectively, and the situation at tail end (number and details of caudal glands, number and arrangement of spinnerets).

But the new genus is also clearly set off from *Echinotheristus* by the absence of both precloacal supplements and of transverse rows of small spines on the cuticular rings. In *Pseudechinotheristus* the amphids show a significant sexual dimorphism in size, though it is not clear, if the amphids are bladder-like or not.

Echinotheristus is mainly characterized by the bladder-like precloacal supplements being reminiscent of structures in limnetic *Tobrius* species (Thun & Riemann, 1967) and the cuticle covered by transverse rows of small spines, thus set off from all other Xyalidae.

Because of the similarity to *Echinotheristus* (i.e. ciliary insecam in the progaster region), but recognizing the difference from it in decisive characters, *Pseudechinotheristus* is erected and refers to that similarity. *Echinotheristus* is known only from sublittoral coarse sands of the North Sea whereas *Pseudechinotheristus* in Australia is found only in intertidal medium to fine sands.

***Pseudechinotheristus nudus* sp. nov. (Fig. 3)**

MATERIAL EXAMINED. HOLOTYPE, QMG218936, ♂, Ayr, Alva Beach, 01.10.1997, embedded in glycerol. D. Blome. PARATYPES, QMG218937, ♂, QMG218938, ♀, and QMG218939, ♀, same data as holotype. OTHER MATERIAL. 28♂, 11♀, 14 g♀, 26 juv., same data as holotype.

ETYMOLOGY. Latin *nudus*, naked - refers to the absence of cuticular spines and bladder-like supplements.

MORPHOMETRIC DATA. ♂₁ (holotype): L = 840 µm; a = 27.1; b = 4.4; c = 7.5; Spicules: 50 µm (left) and 41 µm (right) on the chord. ♂₂: L = 856 µm; a = 25.2; b = 4.3; c = 8.6; Spicules: 52 µm (left) and 42 µm (right) on the chord. ♀: L = 864 µm; a = 22.7; b = 4.3; c = 8.3; V = 71.3%. juv.: L = 936 µm; a = 22.3; b = 4.1; c = 8.5; V = 71.8%.

DESCRIPTION. Body moderately slender, approximately continuous in width, only slightly tapering towards the anterior end, but most prominent from the amphids anteriorly.

Males (mainly referring to holotype): Cuticle coarsely annulated, anterior to the amphids more finely as well as immediately before the spinnerets. Annules with faint longitudinal striae, which sometimes appear to be dot-like. Small spines, arranged in transverse rows, never seen. Longitudinal rows of submedian setae from the posterior end of amphids towards the tail. Setae in the neck region, especially at cardia, longer than

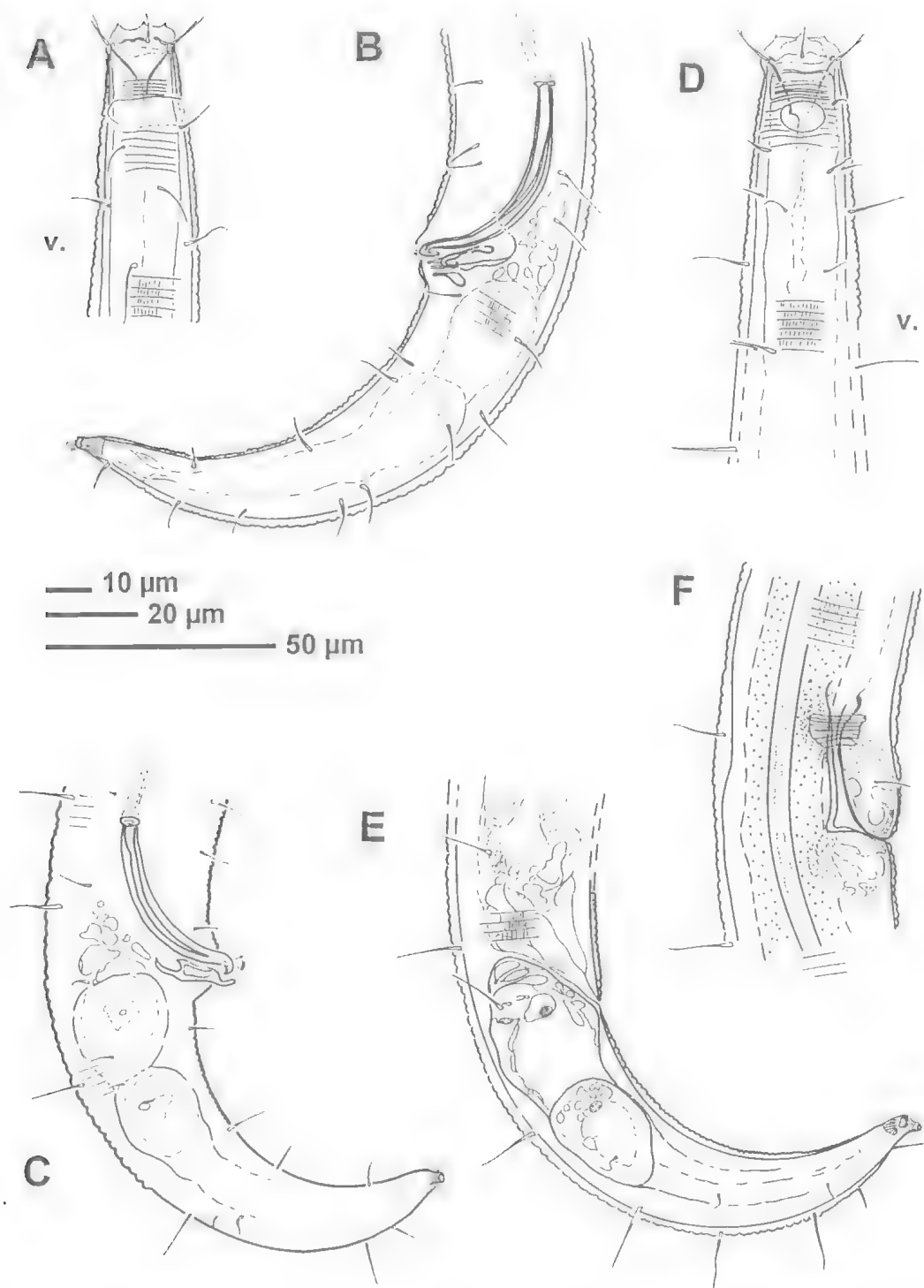


FIG. 3. *Pseudechinotheristus nudus* gen. et sp. nov. A-B, ♂, holotype: A, head; B, tail region and spicular apparatus from the left. C, ♂, paratype 2: tail region and spicular apparatus from the right. D-F, ♀, paratype 1: D, head; E, tail region; F, vulvar region. (v = ventral side).

rest of the body setae: the subventral setae measuring 12–13 µm, the subdorsal ones 13–15 µm. Other body setae measuring 8 µm subventrally and 12 µm subdorsally. Amphids bladder-like? Contours inconspicuous, marked by the absence of cuticular annulation mainly, broadly transverse, covering the total width of the body, i.e. at least 100% of the corresponding diameter (c.d. ~ 18 µm). They are situated 16 µm (~ 1 h.d.) posterior to front end and are 7–9 µm long. Six acute, conical labial sensillae in R_1 , 6 + 4 cephalic setae in one ring measuring 6 and 9–10 µm in length. Buccal cavity with prominent ring in anterior part and with funnel-shaped transition to the oesophagus. Dorsal wall for a stretch of 12–13 µm more sclerotized than the ventral one. Cardia small, glandular. Progaster lined by a ciliary insecum. Ventral gland not seen, but in ♂₂ an (exit?) pore at 76 µm posterior to head end. Testes opposed, outstretched. Anterior testis situated subventrally to the left of intestine, posterior one to the right of intestine. Vas deferens ventral to intestine, appears glandular. Two long-stretched ejaculatory glands in tandem, at each side of the intestine subdorsally. Spicules slightly asymmetrical as to their length, well cuticularised and regularly bent; distally recurved-bifurcated, proximally surrounded by a ring-shaped bulge. Lateral pieces well cuticularised and distally bifurcated as well; proximally, from the dorso-caudal branch sending a membranous process anteriad, passing the spicules laterally. No supplements or ventromedian preloaeal differentiations. Tail conical with two large caudal glands, opening into two separate conical outlets with two separate ampullae. Bases of the outlets with radial striae. Cell-bodies of the caudal glands filled with thread-like or laminar structures. Tip of tail bent to the left.

Females (paratypes): General body shape similar to the males. Amphids transversely oval, inconspicuous, 13–15 µm behind anterior end and 6–7 µm long. They have 40–50% of the corresponding diameter in width. The 10 (R_2 + R_3) cephalic setae are of 6–8 and 10 µm length. Buccal cavity as in males. Cardia small, conoid (heart-shaped) and about 11 µm long. In the progaster filamentous structures visible, lumen of intestine covered by a hyaline layer. Ventral gland not seen, but in ♀₂ an (exit?) pore about 76 µm posterior to head end. Gonad monodelphic with an outstretched ovary left of intestine; no postvulvar structures. Germinal zone of ovary about 200 µm behind anterior end. Distal part of

the gonad (80 µm anterior to proximal part of vagina) appears swollen, thin-walled, and contains spherical to ovoid sperms with hyaline, dotted outline; probably acting as spermatheca. Measurement of a sperm: 6 × 4 µm. Vagina with an anterior and posterior vulvar gland, about 34–37 µm long, and with a well cuticularised inner lining. Proximally surrounded by a circular sphincter. Vulvar lips without prominent structures like small papillae. Tail as in males.

DIAGNOSIS. As for genus.

Dactylaimoides gen. nov.

DIAGNOSIS. Cuticle coarsely annulated, notched; in oesophageal region dark, the margins of annules directed anteriad. At short distance behind amphids six longitudinal crests begin consisting of arched and quadratic elements, having a point of reversal in pattern. Amphids circular, showing sexual dimorphism in size, shape, and position. From the cephalic sensillae only six stout setae visible. Buccal cavity nearly cylindrical with a conspicuous, light refractive, crown-like ring bordering the anterior part of it and demarcating it from the very hyaline, high lip region. Ventral gland not seen. Due to the state of preservation no details of the male gonad visible: possibly two opposed testes, the anterior one to the left of intestine. Spicular apparatus weakly cuticularised, relatively simple. Spicules strongly curved, distally with subterminal denticles (claws?), gubernaculum inconspicuous. Female gonad monodelphic with an anterior outstretched ovary left to intestine. Tail conical, plump; with a typical broad tip, surrounded by a hyaline collar. Three caudal glands ending in one common outlet.

TYPE SPECIES. *Dactylaimoides coronifer* sp. nov.

ETYMOLOGY. Similar to *Dactylaemus* Cobb, 1920, especially in the head region.

DISCUSSION. *Dactylaimoides* is a member of the Xyalidae, mainly because of the arrangement of the gonads: two opposed testes in the male, at least the anterior one to the left of intestine and, in the female, one anteriorly directed outstretched ovary at the left of intestine.

Within the Xyalidae *Dactylaimoides* belongs to the group with coarsely annulated cuticle plus longitudinal ornamentation showing V- or otherwise shaped structures, sometimes possessing a point of reversal (*Xenolaimus* Cobb, 1920; *Xyala* Cobb, 1920; *Gonionchus* Cobb, 1920 part or

Corononema Nicholas & Stewart, 1995) – in this respect being reminiscent of characters known from Monoposthiidae, but differing from the latter family clearly by the absence of teeth, a posterior oesophageal bulb and finally in the conditions of the female gonad(s) (outstretched versus reflexed).

The head, lips and amphids have similarities with *Dactylaimus* but also with the *Xenolaimus*/*Cenolaimus* complex. In *Dactylaimus* these refer in particular to peculiarities in the organization of the lip region. In *Xenolaimus* these concern the coarse, complicated cuticle (with point of reversal in the longitudinal cuticular ornamentation), peculiarities in the lip region ('thick, somewhat digitate lips', Cobb, 1920), and the 'buccal cavity wide and deep, with two weakly cuticularised teeth or cuticular folds projecting from the base of the mouth to the base of the lips' (Wieser & Hopper, 1967).

Xenolaimus is set off from the new genus in having a cuticle with V-shaped structures arranged in longitudinal rows and the first cuticular annule being wider than the following ones. The head is set off, protrusible, surrounded by a 'balustrade' (Cobb, 1920; see also *Omicronema coronalata* Stewart & Nicholas, 1994). Further it is characterized by $6 + (6+4)$ cephalic sensillae, amphids located in an enlarged portion of the fifth annule, and asymmetries in the spicular apparatus. *Xenolaimus* does not have that conspicuous crown-like ring in the buccal cavity, typical for *Dactylaimoides*.

Xenolaimus pauroamphus Nichols, 1979, the only further species in this genus, has to be regarded as a doubtful species because of the absence of the V-shaped cuticular ornamentation and the lack of gubernacula as well as apophyses.

Cenolaimus Cobb, 1933, based on the original diagnosis, is mainly separated from the new genus in having 'deep striae grooving the cuticle, wings none', 'spicula (or more likely) the thin, parallel accessory pieces bifurcated distally', and 'setae at base of spinneret three to four times as long as its diameter'. Unfortunately the original diagnosis and description of *C. supersensitens* Cobb, 1933 from New Caledonia is rather scanty and lacks drawings. Cobb himself mentioned the resemblance to *Omicronema*, but decided to establish the new genus for several justified reasons. Because of the altogether insufficient description *Cenolaimus* Cobb, 1933 has to be regarded as a genus inquirendum.

Cenolaimus, as understood by Nichols when describing *C. sapeloensis* Nichols, 1979, differs from Cobb's (1933) definition mainly in characters as: cuticle with prominent longitudinal 'striations', labial sensillae setiform (resembling *Xyala*, as does the setation at the head end of her species in general), the lack of long setae at base of spinneret, and well cuticularized spicules and well developed gubernaculum with dorsally directed apophysis (resembling *Xyala*).

C. sapeloensis Nichols, 1979 appears not to be a *Cenolaimus* sensu Cobb, 1933 and seems rather to belong to the group of Xyalidae next to *Xyala* or *Gonionchus*; hence it has to be regarded as a species inquirenda.

Xyala is separated from the new genus by high, hyaline lips without flap-like protrusions, a cuticle with rectangular projections in longitudinal rows aligned to form crests (Stewart & Nicholas, 1994), and a relatively shallow buccal cavity with a short parallel sided rigid part.

Gonionchus differs in having high, hyaline lips their apical parts ending in flap-like protrusions, a conical buccal cavity surrounded by oesophageal tissue, ventrosublateral tooth-like projections, a cuticle with or without longitudinal ornamentations (but never showing V-shaped or arched structures), and spicules with a bifid tip (generic character according to Vincx, 1986).

Dactylaimoides is mainly characterized by the coarse complicated cuticle with longitudinal crests built by arched and rectangular structures and the peculiar strongly light refractive, crown-like buccal ring, the sexual dimorphism in size and position of the amphids, and the typical broad tail tip, surrounded by a hyaline collar.

***Dactylaimoides coronifer* sp. nov. (Fig. 4)**

MATERIAL EXAMINED. HOLOTYPE, QMG218940, ♂₁, Innisfail, Forrest Beach, 28.09.1997, embedded in glycerol. D. Blome. PARATYPES, QMG218941, ♂₂, QMG218942 ♀₁, and QMG218943, ♀₂, same data as holotype. OTHER MATERIAL: 3 ♂, 3 ♀, 8 juv. - Ingham, Forrest Beach; 1 juv. - Ayr, Alva Beach, 01.10.1997. D. Blome.

ETYMOLOGY. Latin *corona*, crown and *ferre*, to bear; referring to the light refractive, crown-like structure in the anterior part of the buccal cavity.

MORPHOMETRIC DATA. ♂₁ (holotype): L = 687 µm; a = 34.4; b = 4.0; c = 7.9; Spicules: 19 µm (left), 18 µm (right) on the chord. ♂₂: L = 768 µm; a = 24.0; b = 3.8; c = 7.9; Spicules: 22 µm (left), 19 µm (right) on the chord. ♀₁: L =

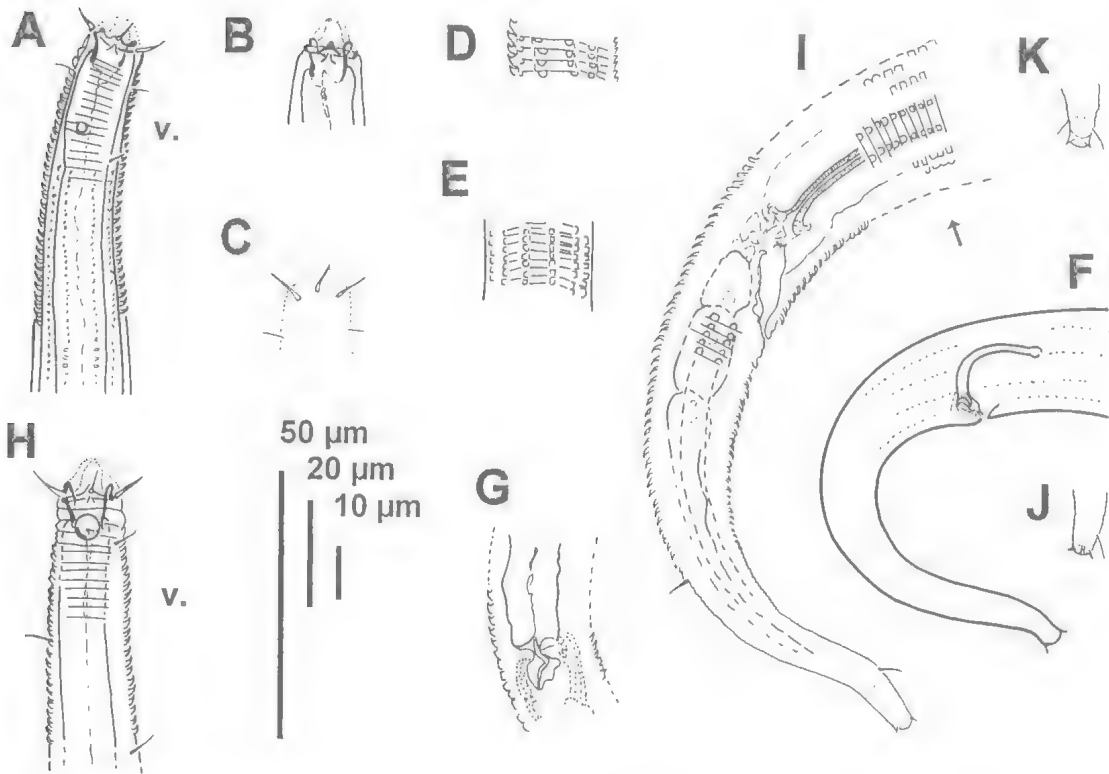


FIG. 4. *Dactylaimoides coronifer* gen. et sp. nov. A-G, ♂, holotype: A, head; B, study of lip region and 'buccal crown'; C, study of setation at head end; D, cuticular structure at end of oesophagus; E, middle of the body-length; F, tail region and spicular apparatus; G, end of oesophagus. H-I, ♀, paratype 1: H, head; I, tail region (arrow points to point of reversal in cuticular pattern). J, male, paratype 2: tail tip. K, ♀, paratype 2: tail tip. (v = ventral side).

800µm; a = 24.2; b = 3.7; c = 8.5; V = 75%. ♀₂: L = 720µm; a = 18.0; b = 3.8; c = 7.5; V = 73%.

DESCRIPTION. Body relatively small, slender, nearly constant in width throughout the body length, tapering towards the extremities.

Males (mainly referring to holotype). Cuticle coarsely annulated, notched. Margins of annules in oesophageal region directed anteriorly. In this region the cuticle is particularly thick, dark, especially anterior to nerve ring. At a short distance behind amphids a differentiation into six crests begins on each side of body consisting of arched structures, the curves of which are directed posteriorly at level of cardia. From the latter the single elements of the crests appear to be square towards the posterior end. Crests ending at about 60% of tail length. A point of reversal in the arched elements of the crests not seen. Amphids inconspicuous, with circular apertures of 2µm in ♂₁, slightly transversely oval

(2.4 x 3.2µm) in ♂₂. Situated 20-22µm posterior to translucent lip region. They have 14 (♂₁) – 23% (♂₂) of the corresponding diameter. Six stout cephalic setae of 6µm (= 0.6 of c.d.) length visible. Level with base of buccal cavity a pair of subcephalic or neck setae. Lips hyaline - hard to recognize, high; measuring about 6µm from base of light refractive ring surrounding the anterior part of buccal cavity. Buccal cavity cylindrical with well cuticularised dorsal and ventral walls. A crown-like strongly light refractive ring with 6 anteriorly directed projections/archs demarcates the anterior part of buccal cavity (9x7µm) from the lip region. At the base of the buccal cavity a projection of the inner oesophageal wall (fold?) is visible, not as conspicuous as in ♀₁. Ventral gland not seen. Due to the state of preservation details of the gonads were never clearly discernable. Possibly there are two opposed testes, the anterior one situated to the left of intestine. Spicules symmetrical, strongly curved,

relatively weakly cuticularised, distally attenuated like a pipette. Just before the distal end two subterminal denticles, one directed laterally, the other one directed caudad. The gubernaculum seems to be a tiny triangular structure at the distal end of the spicular pouch. Tail conical, plump (= 4.5 of cloacal diameter), broad at tip, which appears to be surrounded by a hyaline collar. Because this is the situation in all individuals, it can be excluded that the tip is wounded or broken. Three inconspicuous, serial caudal glands. In ♂₂ 4 small, fleshy, broad-based but pointed terminal setae flank the spinneret - possibly papillae, forming a kind of hyaline collar? One terminal seta, subventrally.

Females (paratypes). The females resemble the males in general appearance. Cuticle in neck region coarser, dark; beginning of crests about 80 µm anterior to cardia; exactly at cardia the very coarse annulation of the anterior end ending. In adanal region the cuticle is also coarser and dark, beginning 46 µm preanally and ending 66 µm behind anus (covering a stretch of 112 µm, altogether). Secondary structures (arches) of crests as in males; a point of reversal of those structures seen only in females at about 2.5 anal diameters anterior to anus (= 50-55% (♀₂) of distance vulva-anus): here the square structures, covering most of all body annules, change to arched structures again, the curves of which are directed anteriorly (cf. Fig. 4I). Amphids strongly sclerotized, circular, with the anterior margins of apertures 11-18 µm behind the very translucent lip region, 5 µm in diameter (35-39% of c.d.). Lips about 6-8 µm high, faint. Six very transparent, little horn-like cephalic setae of 8 µm length (= 0.7 of c.d.). Never more than those six setae observed. Buccal cavity in its basal part slightly funnel shaped, with thickened walls, measuring 10 µm in length and 7 µm in width at maximum. At base of the buccal cavity there is a projection of the inner ventral oesophageal wall (fold?) as in male. Gonad monodelphic; ovary outstretched and directed anteriorly, situated to the left and dorsal of the intestine. Germination zone about 140 µm behind cardia. Vulva inconspicuous. Tail as in males. In ♀₂ a subdorsal terminal seta seen (Fig. 4K), but that seta was not seen in all specimens (probably broken?). Three caudal glands.

DIAGNOSIS. As for genus.

Paragonionchus gen. nov.

DIAGNOSIS. Cuticle coarsely annulated, notched; margins of annules directed anteriorly. In cardiac region 8-10 longitudinal crests begin, consisting of rectangular projections, and ending on tail, when its cylindrical part begins. Amphids inconspicuous, circular, cryptospiral. Cephalic sensillae in three separate rings, with R₃ far behind at level with amphids. Buccal cavity in its major part cylindrical, wide; in its posterior part tapering conically. Cylindrical part with strongly cuticularised strips. Oesophagus inserting at posterior end of cylindrical part of stoma wall. Lips transparent, deeply incised and with complicated cuticularised supporting elements. Ventral gland not seen. Male gonad diorchic; testes opposed, outstretched, posterior one to the right of intestine. Anterior testis possibly to the left of intestine. Spicules regularly bent, proximal ends less cuticularised than the distal, more robust parts. Gubernaculum complicated, close to the spicules, the latter laterally enclosing with protrusions. Tail slender, conical in its anterior part, short cylindrical terminal part. Three slender caudal glands.

TYPE SPECIES. *Paragonionchus sclerolabiatum* sp. nov.

ETYMOLOGY. Greek *para-*, close to, near; similar to *Gonionchus* Cobb, 1920.

DISCUSSION. This new genus also belongs to that group of Xyalidae with strongly annulated cuticle forming longitudinal crests or cuticular ornamentations made of peculiar shaped projections, i.e. *Xyala* Cobb, 1920; *Xenolaimus* Cobb, 1920 and *Gonionchus* Cobb, 1920 (ptm.). *Omicronema* Cobb, 1920 and *Cenolaimus* Cobb, 1933, both also having strongly annulated cuticles, are easily separated by the absence of rectangular projections or longitudinal crests. *Corononema* Nicholas & Stewart, 1995, which has eight longitudinal ridges on its strongly annulated cuticle does not have angular projections on them, and *Xenolaimus* is among others characterized by V-shaped cuticular structures forming longitudinal rows with a point of reversal.

Xyala is separated from the new genus by high, hyaline lips (Stewart & Nicholas, 1994) (without flap-like protrusions) and a buccal cavity with a relatively low (often wider than long), sclerotized cylindrical part, never surrounded by oesophageal musculature and never with cuticular tooth-like projections (Vincx, 1986; Vincx & Furstenberg, 1988).

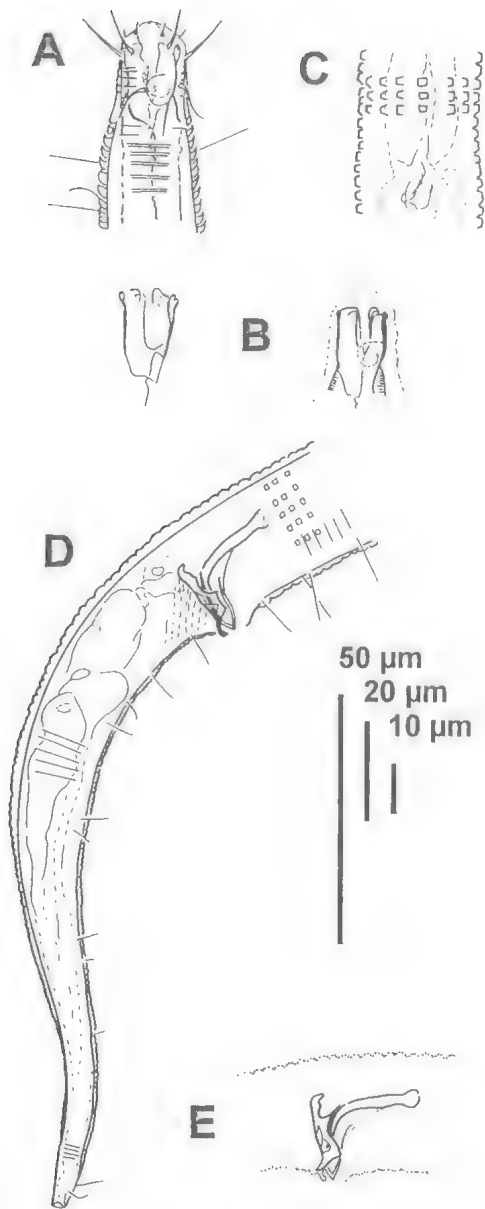


FIG. 5. *Paragonionchus sclerolabiatu* gen. et sp. nov. A-E, ♂, holotype: A, head; B, studies of the sclerotized structures in buccal cavity and lip region; C, cuticular structure in cardia region; D, tail region and spicular apparatus; E, spicular apparatus.

Gonionchus differs in having high, hyaline lips with their apical parts ending in flap-like protrusions, a conical buccal cavity (never with a rigid cylindrical part) surrounded by oesophageal musculature, ventrosublateral tooth-like projections (always recognizable), and spicules

with a bifid tip (see Vincx, 1986). According to Vincx (1986) *Gonionchus* contains three species with longitudinal ornamentation (rectangular projections) of the cuticle (*G. heipi*, *G. longicaudatus*, and *G. sensibilis*) to be supplemented by *G. alastairi* Stewart & Nicholas, 1994. But all of them are true members of *Gonionchus* and hence are clearly differentiated from the new genus.

The deeply incised lips with cuticularised structures (archs, clasps, strips) in the new genus are unique within the Xyalidae. Genera with comparable deeply incised lips are known from families of the Enoplida: Thoracostomopsidae (e.g. *Enoploides* Ssaweljev, 1912; *Met-enoploides* Wieser, 1953), Enchelidiidae (e.g. *Ditlevsenella* Filipjev, 1927) or Tripyloididae (e.g. *Bathylaimus* Cobb, 1894).

Divergent from the general 6 + 10 pattern in the arrangement of the cephalic sensillae of Xyalidae (exception being *Rhynchonema* Cobb, 1920 part, Lorenzen 1981: 240) the new genus shows a pattern of 6+6+4 setae, arranged in three separate rings, being comparable in this respect with the situation in *Dactylaimus* Cobb, 1920 and, possibly, in *Dactylaimoides* gen. n., though in the latter only 6 + 4 setae were visible in two separate rings (the first ring of six (apical) labial sensillae probably hidden due to contraction of the lips or broken?).

***Paragonionchus sclerolabiatu* sp. nov.**
(Fig. 5)

MATERIAL EXAMINED. HOLOTYPE, QMG218944. ♂₁, Port Macquarie, Shelly Beach, 03.09.1997, embedded in glycerol. D. Blome. PARATYPE, QMG218945, ♂₂, same data as holotype. No other material.

ETYMOLOGY. Greek *skleros*, hard; Latin *labium*, lip; deeply incised lips supported by special sclerotized structures.

MORPHOMETRIC DATA. ♂₁ (holotype): L = 1032 µm; a = 36.9; b = 4.7; c = 7.5; Spicules 25 µm on the chord. ♂₂: L = 860 µm; a = 28.7; b = 4.7; c = 7.6; Spicules 24 µm on the chord.

DESCRIPTION. Body slender, tapering towards the extremities, but being between cardia and cloaca nearly equal in width. Only at head end attenuated to 50% of maximum body width.

Males (mainly referring to holotype). Cuticle strongly annulated, in neck region more prominent; margins of the annules directed anteriorly until about 50 µm before cardia (= 77% of oesophageal length). Longitudinal

ornamentation starts about that level with 8-10 longitudinal crests (in lateral view) of rectangular projections. Those crests end on the tail when its cylindrical part begins. Body setation scarce, irregular; immediately behind head several setae, ventral ones measuring $14\mu\text{m}$, the dorsal ones $12\mu\text{m}$, and at neck $8\mu\text{m}$; other body setae $8\mu\text{m}$, in precloacal region $8\mu\text{m}$, and on tail $8\mu\text{m}$ decreasing to $4\mu\text{m}$.

Amphids inconspicuous, circular, cryptospiral; situated $12\mu\text{m}$ behind very hyaline lips/anterior end, $3\mu\text{m}$ in diameter (= 24% of c.d.).

Lip-tips transparent (weakly cuticularised), $4\mu\text{m}$ high (measured from anterior end of thickened parts of buccal wall) Six deeply incised lips with cuticularised archs, clasps, strips. Flap-like protrusions at the apical parts – as usual in *Gonionchus* species – absent. Six delicate, hardly visible labial setae of $2\mu\text{m}$ length followed by a ring of six slender, hyaline cephalic setae (R_2) of $12\mu\text{m}$ length. Four hardly visible, hyaline cephalic setae level with amphids (R_3) of at least $8\mu\text{m}$ length.

Buccal cavity mostly (anterior part) wide, cylindrical, conically tapering at base, measuring $18 \times 9\mu\text{m}$. Cylindrical part with strongly cuticularized strips of $18\mu\text{m}$ length each. Oesophageal musculature inserting at posterior end of cylindrical part of stoma wall. Oesophagus mostly uniformly in width, only slightly widened at posterior end. Cardia oblong, slender heart-shaped. Ventral gland not seen. Gonad diorchic. Testes opposed, outstretched; posterior one situated to the right of intestine; anterior one to the left of intestine? Spicules equal, nearly rectangularly bent. Proximal end up to the knee-shaped curve weakly cuticularised, distal part stronger cuticularised and ending in a widened, V-shaped to sagittiform tip. Gubernaculum strongly cuticularised, close to the spicules, folding up at the sides with protrusions and laterally enclosing them; distally ending with claw-like hook, proximally with free dorsal apophysis. Total length: $17\mu\text{m}$.

Tail conical in its anterior part, then cylindrical. Three slender, serial caudal glands. Two subventral caudal setae of $4\mu\text{m}$ length.

DIAGNOSIS. As for genus.

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LITERATURE CITED

- BLOME, D. 1983. Ökologie der Nematoda eines Sandstrandes der Nordseeinsel Sylt. Mikrofauna des Meeresbodens 88: 1-76.
- COBB, N.A. 1920. One hundred new nemas (type species of 100 new genera). Contributions to a Science of Nematology (Baltimore) 9: 217-343.
1933. New nemic genera and species, with taxonomic notes (Ed. by Margaret V. Cobb). The Journal of Parasitology 20: 81-94.
- FURSTENBERG, J.P. & VINCX, M. 1988. *Procacacolaimus tubifer* Gerlach, 1953, *Procacacolaimus africanus* sp. nov. and *Eontolaimus capensis* gen. nov., sp. nov., (Nematoda, Leptolaimidae) from South Africa. South African Journal of Zoology 23: 208-214.
- GERLACH, S.A. 1953a. Recherches sur la faune des eaux interstitielles de Madagascar. III. Sur quelques Nématodes libres des eaux souterraines littorales de Madagascar. Mémoires de l'Institut Scientifique de Madagascar (A) 8: 73-86.
- 1953b. Die Nematodenbesiedlung des Sandstrandes und des Küstengrundwassers an der italienischen Küste. I. Systematischer Teil. Archivio Zoologico Italiano 37: 517-640.
1954. Les Nématodes marins libres des eaux souterraines littorales d'Espouende (Portugal). Vie et Milieu 4: 83-94.
1962. Freilebende Meeresnematoden von den Malediven. Kieler Meeresforschungen 18: 81-108.
- GERLACH, S.A. & RIEMANN, F. 1973/1974. The Bremerhaven checklist of aquatic nematodes. A catalogue of Nematoda Adenophorea excluding the Dorylaimida. Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven, Supplement 4, Part 1 (1973) and Part 2 (1974): 1-736.
- HOPE, W.D. & TCHESUNOV, A.V. 1999. *Smithsoninema inaequale* n.g. and n.sp. (Nematoda, Leptolaimidae) inhabiting the test of a foraminiferan. Invertebrate Biology 118: 95-108.
- LORENZEN, S. 1981. Entwurf eines phylogenetischen Systems der freilebenden Nematoden. Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven, Supplement 7: 1-472.

- NICHOLS, J.A. 1979. The occurrence of the subfamily Xyalinae (Nematoda, Monhysteroidea) in the Georgia Bight with a description of two new species. *Cahiers de Biologie Marine* 20: 151-159.
- NOLDT, U. & WEHRENBURG, C. 1984. Quantitative extraction of living Plathelminthes from marine sands. *Marine Ecology Progress Series* 20: 193-201.
- PASTOR DE WARD, C.T. 1985. Free-living marine nematodes from the Deseado River estuary (Chromadoroidea: Chromadoridae, Ethmolaimidae, Cyatholaimidae and Choniolaimidae) Santa Cruz, Argentina. 5. Publicación Especial del Centro Nacional Patagónico 6: 1-83.
- PLATT, H. & WARWICK, R.M. 1988. Freelifving Marine Nematodes. Part II. British Chromadorids. *Synopses of the British Fauna (New Series)* No. 38, 502 pp. (E.J. Brill/Dr. W. Backhuys: Leiden).
- STEWART, A.C. & NICHOLAS, W.L. 1994. New species of Xyalidae (Nematoda: Monhysterida) from Australian ocean beaches. *Invertebrate Taxonomy* 8: 91-115.
- THUN, W. VON & RIEMANN, F. 1967. *Echinotheristus* nov. gen. (freilebende Nematoden: Monhysteridae) aus sublitoralem Grobsand der Nordsee. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven* 10: 227-237.
- VINCX, M. 1986. Free-living marine nematodes from the Southern Bight of the North Sea. I. Notes on species of the genera *Gonionchus* Cobb, 1920, *Neochromadora* Micoletzky, 1924 and *Sabatieria* Rouville, 1903. *Hydrobiologia* 140: 255-286.
- VINCX, M. & FURSTENBERG, J. 1988. Three new Xyalidae species (Nematoda) from South Africa, with a redefinition of the genus *Xyala* Cobb, 1920. *Cahiers de Biologie Marine* 29: 497-512.
- WARWICK, R.M. & COLES, J.W. 1975. Notes on the free-living marine genus *Euchromadora* de Man, 1886 and its allies, with description of two new species (Chromadoridae: Nematoda). *Journal of Natural History* 9: 403-412.
- WIESER, W. & HOPPER, B. 1967. Marine nematodes of the east coast of North America. I. Florida. - *Bulletin of the Museum of Comparative Zoology at Harvard College* 135: 239-344.



RECORDS OF THE GREAT-BILLED HERON *ARDEA SUMATRANA* RAFFLES, 1822 FROM THE TIN CAN BAY AREA, SOUTHERN QUEENSLAND

MARK BURNHAM, IAN GYNTHY AND ROD HOBSON

Burnham, M., Gynthy, I. & Hobson, R. 2002 5 31: Records of the Great-billed Heron *Ardea sumatrana* Raffles, 1822 from the Tin Can Bay area, southern Queensland. *Memoirs of the Queensland Museum* 48(1): 45-48. Brisbane. ISSN 0079-8835.

In March and May 2000, incidental sightings of Great-billed Heron *Ardea sumatrana* were made in the Tin Can Bay area, situated at the southern end of the Great Sandy Strait close to the southern tip of Fraser Island. Two further sightings from this mainland locality resulted from a concentrated search in December 2000. These are the first records of *A. sumatrana* from this region since the 1950s when nesting was observed 60-70km to the north on Fraser Island. The temporal and spatial patterns of the present sightings suggest *A. sumatrana* is resident in the Tin Can Bay area, making this the most southerly population recorded in Australia over the past century. The discovery represents a significant southward extension to the Great-billed Heron's current Australian and global distributions. □ *Ardeidae*, *Ardea sumatrana*, southern Queensland, Great Sandy Strait, estuarine areas.

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The Great-billed Heron *Ardea sumatrana* occurs from Burma and Thailand through Southeast Asia and Indonesia to New Guinea and Australia (Hancock & Kushlan, 1984). Although historically the species ranged as far south as NE New South Wales (Ramsay, 1888; Campbell, 1900), an individual recorded there in recent times (Gibson, 1981) is considered to have been vagrant or accidental (Marchant & Higgins, 1990; Pizzey & Knight, 1997). The accepted southern extent of the species post-1900 is the Great Sandy Strait coast of Fraser Island (25°15'S, 153°03'E), based on nesting records (Beruldsen, 1980) originating from the diary of the late Valdie Christensen in the early 1950s (G. Beruldsen, pers. comm.). Importantly, the Queensland Museum's collection does not contain skins or eggs of *A. sumatrana* from Fraser Island (A. Amey, pers. comm.); the records from this locality attributed to D.P. Vernon in Blakers et al. (1984) and Marchant & Higgins (1990) very likely refer to those of V. Christensen (D.P. Vernon, pers. comm.).

Over the ensuing half century since Christensen's records, no additional observations of *A. sumatrana* from the Great Sandy Strait have come to light. The current distribution of the species along the east Australian coast is usually given as Cape York to Broad Sound (22°25'S, 149°45'E; Marchant & Higgins, 1990) or the Rockhampton area (23°30'S, 150°55'E;

Hancock & Kushlan, 1984; Pizzey & Knight, 1997), although more southerly sightings are documented at Eurimbula National Park (24°12'S, 151°48'E; Marchant & Higgins, 1990, where this locality is stated as 'Miriam Vale'; N.G. McKilligan, pers. comm.; D.H.C. Seton, pers. comm.) and the Biloela (Jambin) area (24°15'S, 150°25'E; Blakers et al., 1984; Marchant & Higgins, 1990). Garnett & Crowley (2000) stated there are no recent records south of Rockhampton and suggested the Australian distribution of *A. sumatrana* has contracted northwards up the east coast.

This paper, describing four separate sightings made during 2000 from the mainland Tin Can Bay area, confirms the continued existence of the Great-billed Heron in the Great Sandy Strait, southern Queensland.

MATERIALS AND METHODS

The general area where the sightings were made possesses numerous mangrove-lined creeks, each characterised by a seaward zone of closed *Rhizophora stylosa* and a landward saltpan, between which closed or open communities of *Avicennia marina* or *A. marina* and *Ceriops tagal* sometimes formed a narrow zone. *Bruguiera gymnorhiza* was occasionally present in open stands. Extensive saline grasslands and stands of sedges were present in the intertidal zone in some places. The upper tidal

reaches of each waterway were lined with a closed *Aegiceras corniculatum* community. Terrestrial vegetation surrounding the coastal wetlands consisted of tall open woodland to tall open forest, generally with *Eucalyptus racemosa*, *Corymbia intermedia* and *E. umbra* as dominants. The closed understorey contained a diverse range of heath species, ferns and sedges.

The first two encounters with *A. sumatrana*, in March and May 2000, occurred incidentally during components of a Water Mouse *Xeromys myoides* survey program being conducted by MB in estuarine areas between Rodds Peninsula and Tin Can Inlet. The survey and reconnaissance work involved in this program entailed negotiating tidal waterways by boat and traversing adjacent areas of mangrove, saltmarsh and saltpan on foot. A subsequent, targeted survey for *A. sumatrana*, conducted from 12–13 December 2000, focused on the locations of the two earlier sightings but also examined other suitable habitat in the general vicinity. During this follow-up work, two parties, each comprising two observers, used boats to search tidal creeks and other waterways to their navigable limits. All areas were visited twice over the two day period. Occasionally, searches of adjacent habitat were also undertaken on foot. Colour aerial photography (1:12,000 scale) proved to be an indispensable aid during the survey. Observations were made with Leica 10x42B binoculars and locations recorded using a Garmin GPS 12 or a Garmin GPS 12XL.

RESULTS

All observations were made in or immediately adjacent to estuarine areas in the Tin Can Bay area within the latitudinal band 25°45'–25°55'S. Precise locations are withheld to minimise potentially negative impacts by bird watchers on this species that is noted for its sensitivity to human disturbance (Seton, 1973; Marchant & Higgins, 1990).

At 12:00 on 10 March 2000, a single adult *A. sumatrana* was observed at an initial distance of approximately 60m as MB and M. Ford walked beside a narrow tidal creek. The bird took flight from the ground within a low mangrove community consisting of *Avicennia marina*, *Rhizophora stylosa* and *Ceriops tagal*. It flew 350m upstream and into woodland adjacent to an area where sedgeland surrounded the creek's mangroves. The bird landed in an unidentified eucalypt where it behaved warily, not allowing an

approach closer than 100m. A photograph taken at this range was sufficient to confirm the identification.

At 14:00 on 21 May 2000, while canoeing around a bend in another small creek 4.4km from the previous sighting, MB and J. Holt observed an adult *A. sumatrana* at close range (10m) as it perched 3m above ground in an *A. marina* amid a fringing, low mangrove community. Startled by the canoe's unexpected approach, the heron flew upstream until out of sight. It was not located again.

The subsequent, targeted survey conducted by four observers yielded two sightings of single *A. sumatrana* on 13 December 2000. At 07:30, MB and RH briefly glimpsed an individual flying downstream beside a section of a third creek 3.2km and 2.4km, respectively, from the locations of the first and second incidental sightings described above. Here, scattered *Aegiceras corniculatum* lined the water's edge. A steep, 10m bank obscured the view of the heron as it flew at 6–8m height, just below the canopy level of the surrounding terrestrial woodland.

At about 11:00 the same day, while searching an area 360m straight-line distance downstream of the site where the March 2000 observation was made (and 3.4km from the location of the earlier observation that morning), IG and K. Wortel sighted an *A. sumatrana* as it flushed from a shallowly-flooded mangrove and saltpan area situated between the creek bank and the dense mangroves lining the creek channel. Mangrove species were *A. marina*, *R. stylosa*, *C. tagal* and *Bruguiera gymnorhiza*. Initial viewing range was approximately 35m as the bird flew parallel to shore at a height of only 3m before veering away to land in a 9m high *Eucalyptus umbra*, some 80m from the creek in the adjacent woodland. The heron perched at 5m on a horizontal limb (Fig. 1) and remained there, watchful, until flushed when IG approached too closely on foot to obtain additional photographs. It then flew only 30m to an exposed, dead branch of a *Melaleuca quinquenervia* where more photographs were taken (Fig. 2). Views with binoculars at ranges down to 30m revealed the bird to be in breeding plumage as indicated by its grey facial skin, nuchal crest, and long plumes on the lower foreneck and back (Marchant & Higgins, 1990; Pizzey & Knight, 1997). After a brief and unrewarded search for nests in the immediate vicinity, the site was departed at 12:20 with the heron still in the same tree.



FIG. 1. *Ardea sumatrana* perched in *Eucalyptus umbra*, Tin Can Bay area, SE Queensland.



FIG. 2. Final perching position of the *Ardea sumatrana* individual, Tin Can Bay area, SE Queensland.

DISCUSSION

That the three sighting dates reported here span a nine month period suggests *A. sumatrana* is resident, not vagrant, in the Tin Can Bay area. Two observations made nine months and just 360m apart on the same creek also suggest a resident individual was involved. The species is known to be solitary and sedentary (Blakers et al., 1984; Hancock & Kushlan, 1984), with probable territory sizes of several square kilometres (Marchant & Higgins, 1990). Previous Queensland studies have found territories are separated by 1.5km (straight-line distance) and 5km (by river) along the same estuarine system (Seton, 1973; Garnett & Bredl, 1985). Consequently, although all our observations involved single birds, the likelihood that more than one individual exists at the locality is supported by sightings made the same morning, but more than 3km apart on different creeks, and by the separation of each of the three general sighting locations by 2.4 to 4.4km. These distances are all straight-line measures – actual separation of the sites by water would be much

greater. Considered together, the results indicate that the area in question may support a small population of Great-billed Herons.

If this assumption is correct, the Tin Can Bay area represents the southernmost locality occupied by *A. sumatrana* in Australia since 1900, being 60-70km south of the previous records from the western shore of Fraser Island (Beruldsen, 1980; V. Christensen via G. Beruldsen, pers. comm.) and approximately 330km south of Rockhampton, often cited as the modern limit of the distribution of this species (Hancock & Kushlan, 1984; Pizzey & Knight, 1997; Garnett & Crowley, 2000). The apparent persistence of a population in the Great Sandy Strait 50 years after it was last noted argues the suggested northward contraction of the species' distribution up the east coast (Garnett & Crowley, 2000) may not have been as extensive as originally thought. Although conclusive evidence of present day nesting of *A. sumatrana* at this locality is not available, extensive areas of suitable habitat along remote and seldom-visited tidal creeks in the Tin Can Bay area, as well as further north along the Great Sandy Strait, offer

ample opportunities for breeding by this species. Additional surveys are required to confirm this possibility and to better define the distribution and abundance of *A. sumatrana* in the region.

ACKNOWLEDGEMENTS

We are especially grateful to the Department of Natural Resources and Mines, Department of Primary Industries (Forestry) and the Australian Defence Force for permitting access to their lands and to Kirsten Wortel for her valuable assistance during the December 2000 survey. Excellent field and logistical support was provided by Jennifer Holt and Michael Ford. Paul Grimshaw kindly identified a botanical specimen. Gordon Beruldsen, Don Seton, Neil McKilligan and Don Vernon generously provided information about previous Queensland records of *A. sumatrana*.

LITERATURE CITED

- BERULDSEN, G. 1980. A field guide to nests and eggs of Australian birds. (Rigby: Adelaide).
- BLAKERS, M., DAVIES, S.J.J.F. & REILLY, P.N. 1984. The atlas of Australian birds. (Melbourne University Press: Melbourne).
- CAMPBELL, A.J. 1900. Nests and eggs of Australian birds. (Pawson & Brailsford: Sheffield).
- GARNETT, S.T. & BREDL, R. 1985. Birds in the vicinity of Edward River Settlement. Part I. Introduction, methods, study area, list of non-passerines. *Sunbird* 15: 6-23.
- GARNETT, S.T. & CROWLEY, G.M. 2000. The action plan for Australian birds 2000. (Environment Australia: Canberra).
- GIBSON, A. 1981. Great-billed Heron at Yamba. *Australian Birds* 16: 32-33.
- HANCOCK, J. & KUSHLAN, J. 1984. The herons handbook. (Croom Helm: London).
- MARCHANT, S. & HIGGINS, P.J. 1990. Handbook of Australian, New Zealand and Antarctic birds. Volume 1. Ratites to ducks. (Oxford University Press: Melbourne).
- PIZZEY, G. & KNIGHT, F. 1997. The field guide to the birds of Australia. (Angus & Robertson: Sydney).
- RAMSAY, E.P. 1888. Tabular list of all the Australian birds. (The author: Sydney).
- SETON, D.H.C. 1973. Observations on breeding of the Great-billed Heron in northern Queensland. *Emu* 73: 9-11.

SPECIES DIVERSITY WITHIN *MACROPODINIUM* (LITOSTOMATEA:
TRICHOSTOMATIA): ENDOSYMBIOTIC CILIATES FROM AUSTRALIAN
MACROPODID MARSUPIALS

STEPHEN L. CAMERON, PETER J. O'DONOGHUE AND ROBERT D. ADLARD

Cameron, S.L., O'Donoghue, P.J. & Adlard, R.D. 2002 5 31: Species diversity within *Macropodinium* (Litostomatea: Trichostomatia): endosymbiotic ciliates from Australian macropodid marsupials. *Memoirs of the Queensland Museum* 48(1): 49-69. Brisbane. ISSN 0079-8835.

Ciliates in *Macropodinium* are the most distinctive component of the ciliate fauna of macropodid marsupials. *Macropodinium moiri*, *Ma. setonixum*, *Ma. ennuensis* forma *ennuensis* and *Ma. yalanbense* are redescribed following silver staining to reveal the arrangement of their ciliary bands. *Macropodinium hallae* sp. nov., *Ma. ocallaghani* sp. nov., *Ma. petrogale* sp. nov. and *Ma. titan* sp. nov. and *Ma. ennuensis* f. *dentis* f. nov., are described for the first time. A new key to the species of *Macropodinium* using light microscopic features of silver stained specimens is provided. Species diversity within the genus (13 species) illustrates the morphological variability within the group and its distinctiveness from other genera of endosymbiotic ciliates. □ *Ciliophora*, *Litostomatea*, *Trichostomatia*, *Macropodiniidae*, *parasite specificity*, *parasite evolution*.

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Most herbivorous mammals are host to a diverse range of ciliated protozoa which inhabit the fermentative digestive organs (Corliss, 1979). Endosymbiotic ciliates have also been detected in macropodid marsupials (kangaroos and their relatives) which are the dominant Australian terrestrial herbivores (Lintern-Moore, 1973; Obendorf, 1984; Dellow et al., 1988; Dehority, 1996; Cameron et al., 2000a; 2000b). Our previous studies have shown that macropodid marsupials are hosts to at least 3 ciliate families: including the Amylovoracidae (Cameron & O'Donoghue, in press); Cycloposthiidae (Cameron et al., 2000); and Macropodiniidae (Cameron et al., 2001). Of these, the monogeneric Macropodiniidae were the most speciose and structurally diverse family with 9 highly host-specific species recovered from 7 host species. The family was originally described by Dehority (1996) on material stained with haemotoxylin, methylene blue and methyl green. This generic diagnosis was amended by Cameron et al. (in press) following studies of material stained with silver proteinate (protargol), which revealed additional structures not described by Dehority (1996). This study re-examines *Macropodinium* spp. described by Dehority (1996) for the new characters described by Cameron et al. (in press) and describes several new *Macropodinium* spp. found in macropodid marsupials.

MATERIAL AND METHODS

Samples of stomach contents were obtained either from road-killed animals or from animals culled from wild populations. The following macropodid species (numbers examined in parentheses) were examined for macropodiniid ciliates: *Macropus eugenii* (14); *M. fuliginosus melanops* (21); *M. fuliginosus fuliginosus* (5); *M. robustus erubescens* (20); *M. robustus robustus* (16); *M. rufogriseus* (32); *Petrogale godmani* (3); and *Setonix brachyurus* (5). Stomach fluid was squeezed from fibrous matter, strained through a triple layer of surgical gauze to remove fine particulate matter and nematodes, and fixed in Bouin's fluid or methyl formol-saline (MFS). Ciliate morphology was determined by microscopic examination of specimens stained with methyl-green, methyl-green pyronin, silver proteinate (protargol), and silver-carbonate (Foissner, 1991). Ciliates were measured using a calibrated eyepiece micrometer and drawn with the aid of a *camera lucida*.

Protargol staining was performed using a combination of the Wicklow & Hill (1992) and Lynn (1992) methods as follows. Cells fixed in Bouin's fluid were washed in distilled water to remove traces of picric acid, dehydrated through a graded series of ethanol solutions (70, 80, 90, 100 and 100% for 10 min each), applied to an albuminised slide and flooded with ethanol.

Evaporation of the ethanol affixes the cells to the albumin. The albumin was fixed by flooding with formol-alcohol (3 parts 10% formaldehyde, 1 part 95% ethanol) followed by immersion in formol-alcohol for 15 min. The specimens were dehydrated in 96% and 100% isopropanol for 2 min each, then immersed in 100% methanol for 3 min. Specimens were coated with 1% parlodion in methanol for 2 sec and air-dried. Slides were coated and air-dried several times, depending on the desired staining effect, rehydrated in a graded series of isopropanol series (70, 50, 30% for 2 min each) and washed two times in distilled water. Cells were oxidised in 0.5% potassium permanganate for 3 min, washed three times in distilled water (for a total of 10 min), bleached in 5% oxalic acid for 5 min and then washed three times in distilled water (for a total of 10 min). Cells were impregnated in 1% protargol at 60°C for 20 min and developed by immersion in 1% hydroquinone dissolved in 2.5% sodium sulphite. Stain development was monitored under a dissecting microscope and halted by

immersion in distilled water. The stain was toned by 1-5 min immersion in 2% oxalic acid, then washed in distilled water for 3 min. For some ciliates, additional toning was achieved by a single dip in 2% gold chloride solution followed by washing in distilled water for 3 min. The stain was fixed by immersion in 5% sodium thiosulphate for 5 min followed by a distilled water wash for 3 min. The specimens were dehydrated through a graded series of isopropanol solutions (30, 50, 70, 96, 100 and 100% for 3 min each), cleared by two washes in xylene and mounted in Depex.

The silver carbonate method of Ito & Imai (1998) was modified as follows. Two drops of MFS fixed ciliates, 3-5 drops of pyridine and 5-7 drops of 4% bacteriological proteose peptone were added to 3 mL of distilled water. The resultant suspension was mixed by inversion and left in a dark box for 20 min. Fifteen to 20 drops of ammoniacal silver carbonate solution (made by mixing 5g of silver carbonate in 5mL of distilled water and solubilising with 25% ammonia; the

TABLE 1. Morphometric characterisation of the macropodiniid ciliate, *Macropodinium moiri* Dehority, 1996 recovered from the quokka, *Setonix brachyurus*; x: mean; SD: standard deviation; CV: coefficient of variation; min: minimum; max: maximum; n: number of observations.

Character	x	SD	CV	min	max	n
Body dimensions						
Length, L	81.0	12.88	15.9	60.8	100.8	20
Width, W	40.8	4.44	10.9	32.8	48.8	20
Shape index (L/W ratio)	2.0	0.20	9.9	1.4	2.3	20
Macronucleus						
Length	14.4	3.18	22.2	9.6	20.8	20
Width	7.3	0.91	12.4	5.6	9.6	20
Micronucleus						
Length	3.9	0.62	15.9	3.2	4.8	14
Width	2.9	0.60	20.5	2.4	4.0	14
Oral apparatus						
Vestibulum width	15.6	2.48	16.0	11.2	19.2	20
Vestibulum depth	24.5	3.38	13.8	16.8	29.6	20
Cytostome width	3.1	0.51	16.4	2.4	4.0	20
Length of oral cilia	6.2	0.76	12.3	4.8	7.2	7
Somatic ciliature						
Length of somatic cilia	6.1	0.92	15.1	5.6	7.2	3
Miscellaneous						
No Longitudinal grooves, Left side	12.6	0.96	7.6	11	15	19
No Longitudinal grooves, Right side	12.6	0.95	7.5	10	14	20
Width between longitudinal grooves	3.2	4.19	12.9	2.4	4.0	19
Depth DB	6.1	0.83	13.6	4.8	8.0	20
Depth VB	8.6	1.61	18.7	6.4	11.2	20
Cytoproct length	5.2	1.31	25.4	3.2	8.0	20

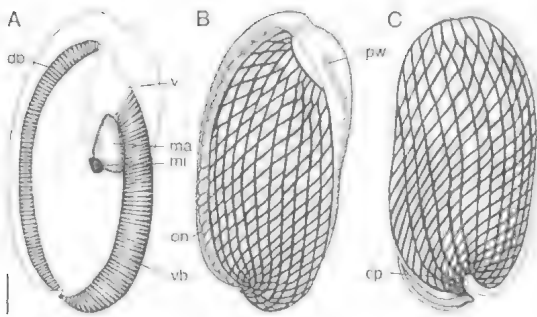


FIG. 1. Morphology of *Macropodinium moiri* Dehority, 1996. A, internal morphology. B, right view, surface features. C, left view, surface features. cp, cytoproct. db, dorsal bars. ma, macronucleus. mi, micronucleus. on, ornamentation. pw, pellicular window. v, vestibulum. vb, ventral bars. Scale bar = 10 μ m.

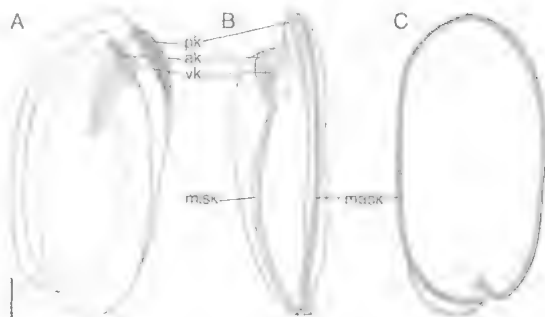


FIG. 2. Infraciliature of *Macropodinium moiri* Dehority, 1996. A, right view, oral ciliary bands. B, ventral view. C, left view, somatic ciliary band. ak, adoral kineties. mask, major somatic kineties. misk, minor somatic kineties. pk, preoral kineties. vk, vestibular kineties. Scale bar = 10 μ m.

resultant solution was made up to 10mL with distilled water) were then added, mixed and the suspension returned to the dark box for 1 hour. The stain was developed by incubation in a 60°C water bath for several hours until the solution turned dark brown (tea-coloured). Ciliates were removed by pipette and examined immediately as wet preparations.

Samples for scanning electron microscopy were fixed in Bouin's fluid, washed with distilled water and separated from gut debris by centrifugation in a discontinuous Percoll gradient (25%, 50%, 75%, 100%) at 3200 g for 10 min. Clean fractions containing ciliates were washed 3 times in Sorensen's phosphate buffer, post-fixed in 4% osmium tetroxide, washed twice in water, dehydrated in a graded ethanol series (30%, 40%, 50%, 60%, 70%, 80%, 90%, 100%, 100%), and dried in a critical-point drier between Millipore filters. Dried cells were sputter-coated with gold and examined in a scanning electron microscope (JOEL 6300). All measurements are given as a range, followed by the arithmetic mean. Summary statistics of morphometrics were prepared using the Statistix® program. Cell orientation and terminology follows that of Cameron et al., (2001). For each species, representative specimens, stained with protargol and mounted on slides, have been deposited with the Queensland Museum, Brisbane (QM). Abbreviations of cellular characters are: DVG, dorso-ventral groove; DB, dorsal bars; VB, ventral bars.

RESULTS

Macropodiniid ciliates were found in 14 (100%) of *M. eugenii* examined; 6 (29%) of *M. fuliginosus melanops*; 3 (60%) of *M. fuliginosus fuliginosus*; 13 (65%) of *M. robustus erubescens*; 9 (56%) of *M. robustus robustus*; 1 (3%) of *M. rufogriseus*; 3 (100%) of *P. godmani*; and 3 (60%) of *S. brachyurus*. Of the ciliates recovered, 4 conformed to species described by Dehority (1996) and are redescribed here to incorporate the features described by Cameron et al. (2001). Another 5 taxa (4 new species and 1 new forma) are described here for the first time.

SYSTEMATICS

Phylum CILIOPHORA Dolfein, 1901
Class LITOSTOMATEA Small & Lynn, 1981
Subclass TRICHOSTOMATIA Bütschli, 1889
Family MACROPODINIIDAE Dehority, 1996
Macropodinium Dehority, 1996

Macropodinium moiri Dehority, 1996
(Figs 1, 2, 3, 10A; Table 1)

MATERIAL. Voucher specimen QMG463137, from the quokka, *Setonix brachyurus* (Quoy & Gaimard, 1830), Rottnest Is., WA 31°59'S, 115°32'E.

DESCRIPTION. Body oval; 60.8–100.8 (81.0) μ m long, 32.8–48.8 (40.8) μ m deep, shape index (L/D) 1.4–2.3(2.0); right side abbreviated compared with left side. Single macronucleus round to globo-triangular; 9.6–20.8(14.4) μ m long by 5.6–9.6 (7.3) μ m wide; located ventral to the vestibulum. Single micronucleus round to oval; 3.2–4.8 (3.9) μ m long by 2.4–4.0 (2.9) μ m wide; adjacent to or obscured by the

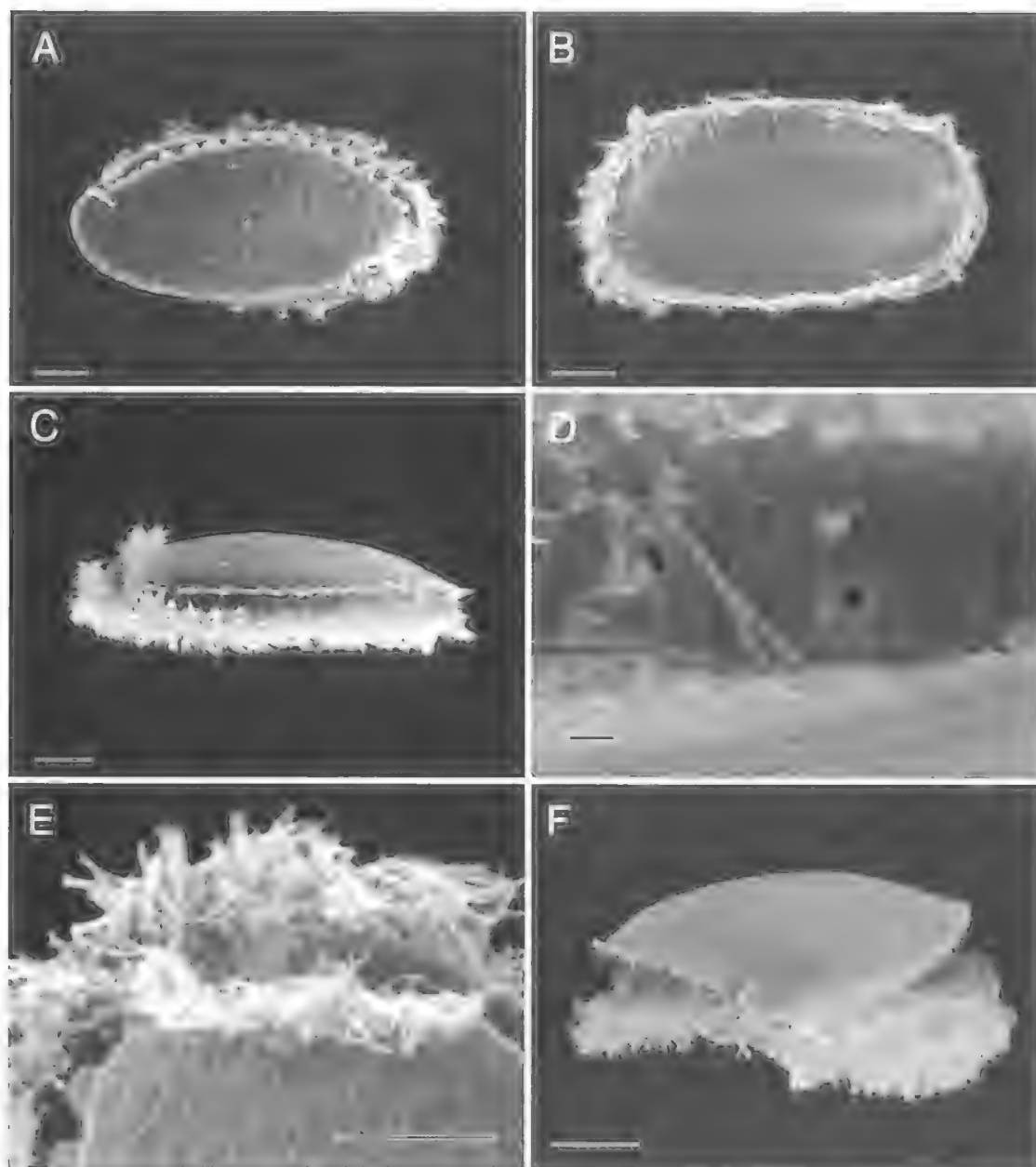


FIG. 3. Scanning electron micrographs of *Macropodinium moiri* Dehority, 1996. A, right view, scale bar = 10 μ m. B, left view, scale bar = 10 μ m. C, dorsal view, scale bar = 10 μ m. D, contractile vacuole pores in ventral DVG, scale bar = 1 μ m. E, anterior right view, scale bar = 10 μ m. F, cytoproct, scale bar = 10 μ m.

macronucleus. Vestibulum conical; 11.2-19.2 (15.6) μ m wide by 16.8-29.6 (24.5) μ m deep; opening apical, directed anterioventrally; cytostome 2.4-4.0 (3.1) μ m wide; cytopharynx composed of short rods directed posteriorly from

the cytostome. Somatic cilia 5.6-7.2 (6.1) μ m long; adoral cilia 4.8-7.2 (6.2) μ m long. Pellicular diamond pattern uniform; left side bears 11-15 (12.6) longitudinal grooves, right side bears 10-14 (12.6) longitudinal grooves; longitudinal

grooves 2.4-4.0 (3.2) μ m apart. DVG deep dorsally and ventrally. DB prominent 4.8-8.0 (6.1) μ m deep; VB prominent 6.4-11.2 (8.6) μ m deep. Flange ornamentations right dorsal. Cytoproct cup-shaped; 3.2-8.0 (5.2) deep; opening posterior.

PREVALENCE. Specimens recovered from 2 of 5 hosts examined.

Macropodinium setonixium Dehority, 1996
(Figs 4, 5, 10B; Table 2)

MATERIAL. Voucher specimen QMG463138, from the quokka, *Setonix brachyurus* (Quoy & Gaimard, 1830), Rottnest Is., WA 31°59'S, 115°32'E.

DIFFERENTIAL DIAGNOSIS. *Ma. setonixium* can be readily distinguished from *Ma. moiri* by its smaller size, anteriorly directed vestibulum and the absence of a preoral window.

DESCRIPTION. Body oval to slightly reniform; 24.8-46.4 (32.1) μ m long by 15.2-24.8 (18.8) μ m

deep, shape index (L/D) 1.3-2.1 (1.7); right side only slightly abbreviated compared with left side. Single macronucleus spherical to ovoid; 4.0-9.6 (6.3) μ m long by 3.2-6.4 (5.0) μ m wide; located ventral or posterior to the vestibulum. Single micronucleus round to oval; 1.6-2.4 (1.6) μ m long by 0.8-1.6 (1.4) μ m wide; adjacent to or obscured by the macronucleus. Vestibulum conical; 4.0-6.4 (5.4) μ m wide by 6.4-11.2 (8.8) μ m deep; opening apical, directed anteriorly; cytostome 0.8-2.4 (1.4) μ m wide. Somatic cilia 4.0-8.8 (5.7) μ m long; adoral cilia 3.2-9.6 (5.8) μ m long. Pellicular diamond pattern uniform; left side bears 7-10 (8.8) longitudinal grooves, right side bears 6-9 (7.1) longitudinal grooves; longitudinal grooves 2.4-4.8 (2.8) μ m apart. DVG shallow dorsally and ventrally. DB prominent 2.4-4.8 (3.4) μ m deep; VB prominent 2.4-4.0 (3.4) μ m deep. No ornamentations. Cytoproct slot-shaped; 1.6-3.2 (2.5) deep; opening posterior.

TABLE 2. Morphometric characterisation of the macropodiniid ciliate, *Macropodinium setonixium* Dehority, 1996 recovered from the quokka, *Setonix brachyurus*; x: mean; SD: standard deviation; CV: coefficient of variation; min: minimum; max: maximum; n: number of observations.

Character	x	SD	CV	min	max	n
Body dimensions						
Length, L	32.1	4.6	14.4	24.8	46.4	20
Width, W	18.8	2.148	11.4	15.2	24.8	20
Shape index (L/W ratio)	1.7	0.20	11.6	1.3	2.1	20
Macronucleus						
Length	6.3	1.2	19.2	4.0	9.6	20
Width	5.0	0.89	17.9	3.2	6.4	20
Micronucleus						
Length	1.6	0.19	11.8	1.6	2.4	17
Width	1.4	0.38	27.5	0.8	1.6	17
Oral apparatus						
Vestibulum width	5.4	0.68	12.6	4.0	6.4	20
Vestibulum depth	8.8	1.25	14.2	6.4	11.2	20
Cytostome width	1.4	0.50	35.2	0.8	2.4	19
Length of oral cilia	5.8	1.68	29.1	3.2	9.6	19
Somatic ciliature						
Length of somatic cilia	5.7	0.99	17.3	4.0	8.8	18
Miscellaneous						
No Longitudinal grooves, Left side	8.8	0.75	8.6	7	10	17
No Longitudinal grooves, Right side	7.1	0.75	10.6	6	9	17
Width between longitudinal grooves	2.8	0.61	22.0	2.4	4.8	20
Depth DB	3.4	0.62	18.0	2.4	4.8	17
Depth VB	3.4	0.45	13.3	2.4	4.0	17
Cytoproct length	2.5	0.53	21.2	1.6	3.2	19

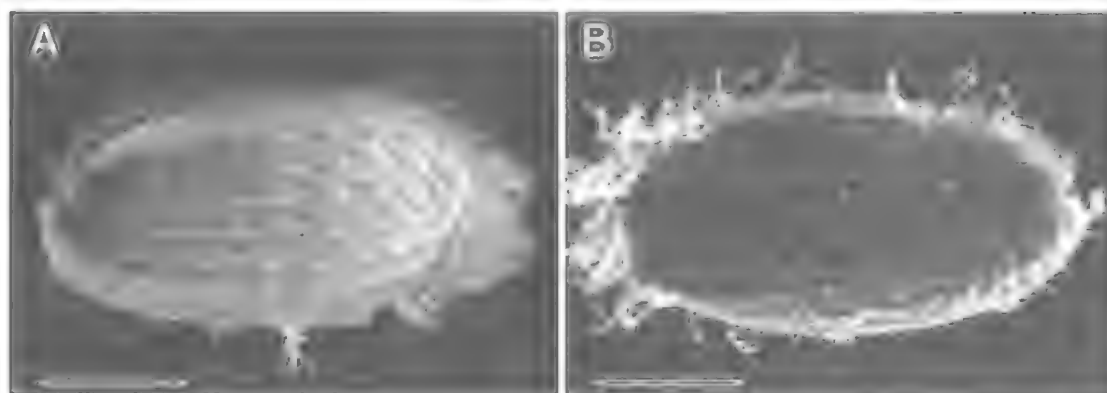


FIG. 4. Scanning electron micrographs of *Macropodinium setonixium* Dehority, 1996. A, right view. B, left view. Scale bars = 10µm.

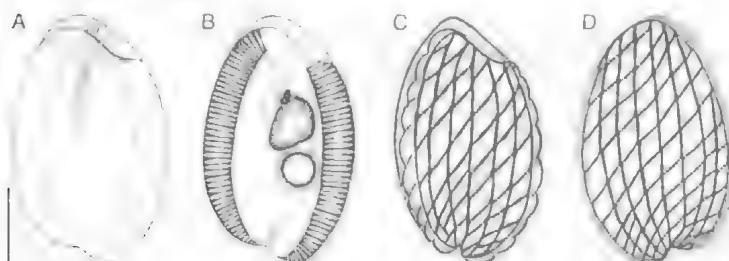


FIG. 5. Morphology and infraciliature of *Macropodinium setonixium* Dehority, 1996. A, infraciliature. B, internal morphology. C, right view, surface features. D, left view, surface features. Scale bar = 10µm.

PREVALENCE. Specimens recovered from 3 of 5 hosts examined.

***Macropodinium ennuensis* Dehority, 1996**
forma *ennuensis*
 (Figs 6, 7A,B, 10C; Table 3)

MATERIAL. Voucher specimen QMG463149, from the euro, *Macropus robustus erubescens* Gould, 1841, Pt Augusta, SA, 32°30'S, 137°46'E.

DIFFERENTIAL DIAGNOSIS. *Ma. ennuensis* possesses a VB but lacks a DB, a feature not shared with any other described species.

DESCRIPTION. The species erected as *Ma. ennuensis* by Dehority (1996) is here redescribed as forma *ennuensis*. Body oval to slightly reniform; 37.6-70.4 (56.2)µm long, 20.0-33.6 (26.4)µm deep, shape index (L/D) 1.5-3.0 (2.1); right side abbreviated compared to left side. Single macronucleus, spherical to ovoid; 5.6-15.2 (9.6)µm long by 4.0-8.8 (6.4)µm wide; located ventral to vestibulum. Single micronucleus, spherical to ovoid; 1.6-3.2 (2.4)µm long by 0.8-3.2 (1.8)µm wide; adjacent

to the macronucleus. Vestibulum bent conical; 8.8-15.2 (11.8)µm wide by 13.6-27.2 (19.0)µm deep; opening subapically, directed anterioventrally. Somatic ciliation 5.6-10.4 (6.7)µm long; adoral cilia 4.0-10.4 (6.7)µm long. Pellicular diamond pattern uniform: left side bears 8-12 (10.3) longitudinal grooves; right side bears 7-10 (8.0) longitudinal grooves; longitudinal grooves 2.4-4.8 (3.4)µm apart. DVG shallow dorsally and ventrally. DB absent; VB prominent, 3.2-7.2 (5.0)µm deep. Ornamentations absent. Cytoproct slot-shaped; 1.6-3.2 (2.5)µm deep; opening posterior.

REMARKS. This forma was also recorded from the euro, *Macropus robustus erubescens* from Spear Creek Stn., SA, 32°34'S, 137°59'E and from the common wallaroo, *Macropus robustus*

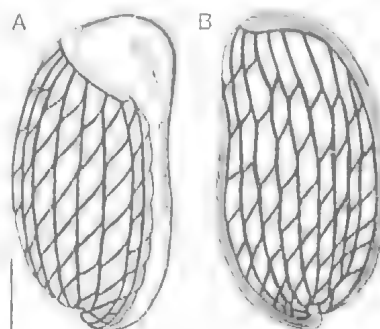


FIG. 6. External morphology of *Macropodinium ennuensis* Dehority, 1996. A, right view. B, left view. Scale bar = 10µm.

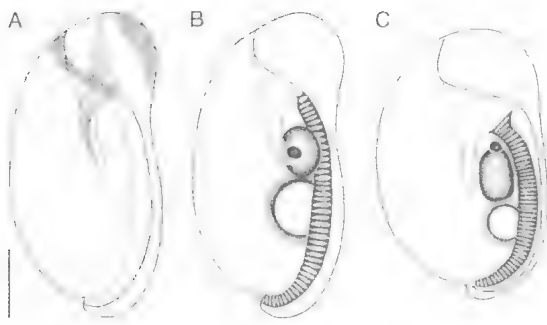


FIG. 7. Infraciliature and internal morphology of *Ma. ennuensis* Dehority, 1996. A, infraciliature. B, internal morphology, *Ma. ennuensis* f. *ennuensis*. C, internal morphology, *Ma. ennuensis* f. *dentis*. Scale bars = 10 µm.

robustus Gould, 1841 on Kilclooney Stn., Qld, 18°50'S, 145°48'E and on Lyndhurst Stn., Qld, 19°12'S, 144°20'E.

PREVALENCE. Specimens recovered from 65% (13 of 20) of euros examined and 13% (2 of 16) of common wallaroos examined.

***Macropodinium ennuensis* Dehority, 1996
forma *dentis* f. nov.
(Figs 7C, 8; Table 4)**

ETYMOLOGY. For the single tooth-like spine on the margin of the vestibulum.

MATERIAL. Voucher specimen QMG463150, from the common wallaroo, *Macropus robustus robustus*, Gould, 1841, Mt. Kinoul, Qld, 25°40'S, 149°40'E.

DIFFERENTIAL DIAGNOSIS. *Ma. ennuensis* f. *dentis* f. nov. is almost identical to *Ma. ennuensis* f. *ennuensis*, with the exception of the spine-like projection off the ventral margin of the vestibulum.

DESCRIPTION. Body oval to slightly reniform; 40.0-70.4 (53.3) µm long, 24.0-32.8 (28.8) µm deep, shape index (L/D) 1.6-2.3 (1.9); right side abbreviated compared with left side. Single macronucleus, spherical to ovoid; 8.0-12.8 (10.1) µm long by 5.6-9.6 (6.8) µm wide; located ventral to vestibulum. Single micronucleus, spherical to ovoid; 2.4-3.2 (2.7) µm long by 1.6-3.2 (2.3) µm wide; adjacent to the

TABLE 3. Morphometric characterisation of the macropodiniid ciliate, *Macropodinium ennuensis* Dehority, 1996 f. *ennuensis* f. nov. recovered from the euro, *Macropus robustus erubescens*; x: mean; SD: standard deviation; CV: coefficient of variation; min: minimum; max: maximum; n: number of observations.

Character	x	SD	CV	min	max	n
Body dimensions						
Length, L	56.2	6.90	12.3	37.6	70.4	80
Width, W	26.4	3.10	11.7	20.0	33.6	80
Shape index (L/W ratio)	2.1	0.23	10.8	1.5	3.0	80
Macronucleus						
Length	9.6	1.90	19.7	5.6	15.2	80
Width	6.4	1.13	17.7	4.0	8.8	80
Micronucleus						
Length	2.4	0.54	22.2	1.6	3.2	34
Width	1.8	0.46	25.2	0.8	3.2	34
Oral apparatus						
Vestibulum width	11.8	1.67	14.2	8.8	15.2	80
Vestibulum depth	19.0	2.60	13.7	13.6	27.2	77
Cytostome width	2.1	0.39	18.6	1.6	2.4	69
Length of oral cilia	6.7	0.86	13.0	5.6	10.4	52
Somatic ciliature						
Length of somatic cilia	6.7	0.98	14.6	4.0	10.4	63
Miscellaneous						
No Longitudinal grooves, Left side	10.3	0.90	8.7	8	12	74
No Longitudinal grooves, Right side	8.0	0.73	9.1	7	10	69
Width between longitudinal grooves	3.4	0.53	15.7	2.4	4.8	79
Depth VB	5.0	0.85	16.8	3.2	7.2	80
Cytoproct length	2.5	0.43	16.8	1.6	3.2	69

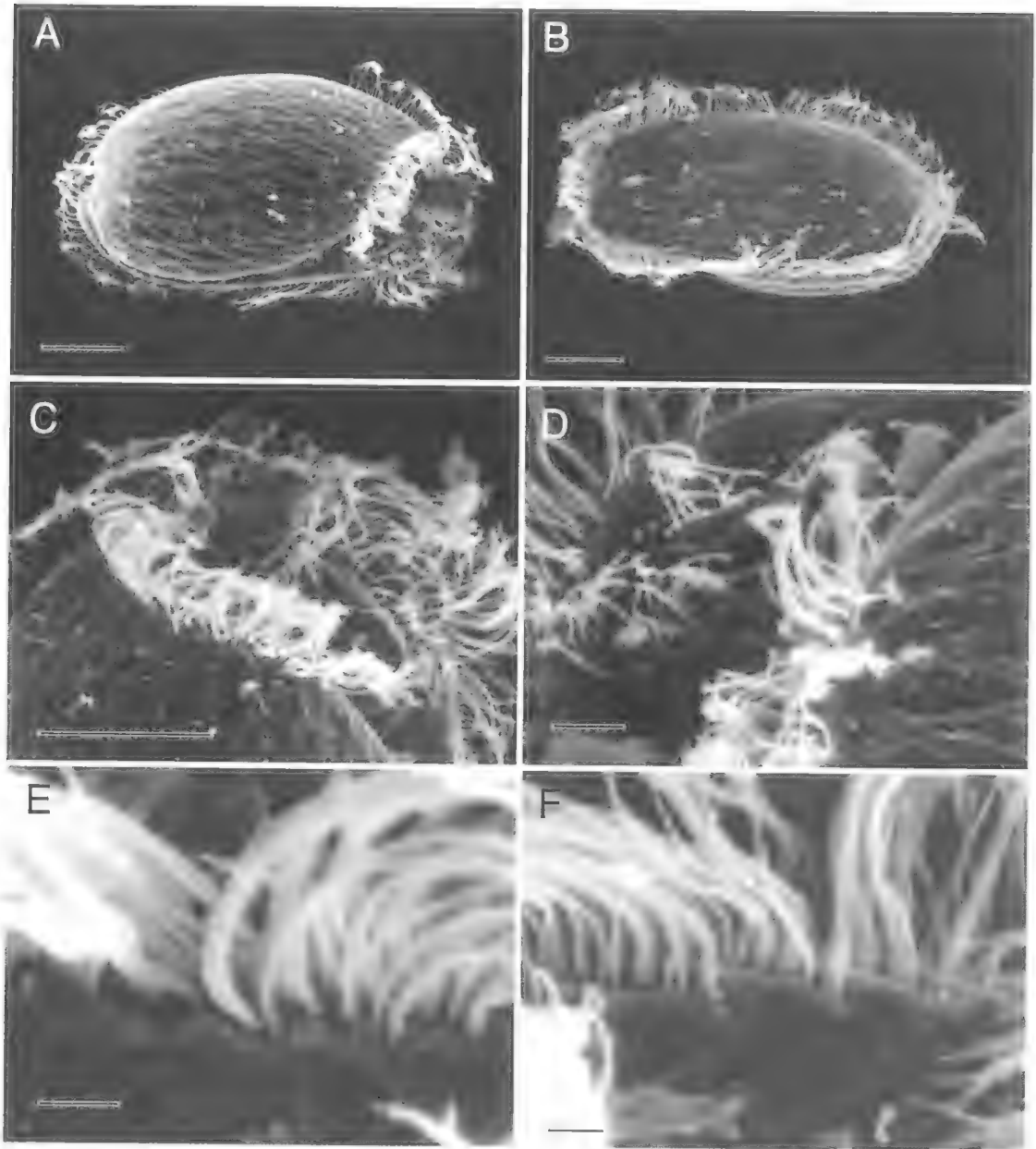


FIG. 8. Scanning electron micrographs of *Macropodinium ennuensis* f. *dentis* f. nov. A, right view, scale bar = 10 μ m. B, left view, scale bar = 10 μ m. C, anterior right view, scale bar = 10 μ m. D, preoral cilia, scale bar = 1 μ m. E, adoral cilia, scale bar = 1 μ m. F, somatic cilia, scale bar = 1 μ m.

macronucleus. Vestibulum bent conical; 7.2-18.4 (11.1) μ m wide by 11.2-22.4 (18.6) μ m deep; opening subapically, directed anteroventrally. Somatic ciliation 4.8-8.0 (6.2) μ m long; adoral cilia 4.8-8.0 (6.2) μ m long. Pellicular diamond pattern uniform; left side bears 9-12 (11.3) longitudinal grooves; right side

bears 9-12 (10.2) longitudinal grooves; longitudinal grooves 2.4-4.0 (3.1) μ m apart. DVG shallow dorsally and ventrally. DB absent; VB prominent, 3.2-6.4 (4.8) μ m deep. Single tooth-like projection within DVG near ventral base of vestibulum. Cytoproct circular; 1.6-3.2 (2.1) μ m deep; opening posterior.

TABLE 4. Morphometric characterisation of the macropodiniid ciliate, *Macropodinium ennuensis* Dehority, 1996 f. *dentis* f. nov. recovered from the common wallaroo, *Macropus robustus robustus*; x: mean; SD: standard deviation; CV: coefficient of variation; min: minimum; max: maximum; n: number of observations.

Character	x	SD	CV	min	max	n
Body dimensions						
Length, L	53.3	5.98	11.2	40.0	70.4	30
Width, W	28.8	2.57	8.93	24.0	32.8	30
Shape index (L/W ratio)	1.9	0.17	9.37	1.6	2.3	30
Macronucleus						
Length	10.1	1.27	12.6	8.0	12.8	30
Width	6.8	0.98	14.5	5.6	9.6	30
Micronucleus						
Length	2.7	0.39	14.6	2.4	3.2	30
Width	2.3	0.35	15.2	1.6	3.2	30
Oral apparatus						
Vestibulum width	11.1	2.25	20.2	7.2	18.4	29
Vestibulum depth	18.6	2.60	14.0	11.2	22.4	29
Cytostome width	2.1	0.40	19.6	1.6	2.4	26
Length of oral cilia	6.2	0.99	16.0	4.8	8.0	19
Somatic ciliature						
Length of somatic cilia	6.2	0.90	14.4	4.8	8.0	21
Miscellaneous						
No Longitudinal grooves, Left side	11.3	0.79	7.0	9	12	30
No Longitudinal grooves, Right side	10.2	0.85	8.3	9	12	30
Width between longitudinal grooves	3.1	0.37	12.0	2.4	4.0	30
Depth VB	4.9	0.66	13.6	3.2	6.4	29
Cytoproct length	2.1	0.47	22.5	1.6	3.2	21

REMARKS. This form was also recorded from *Macropus robustus robustus* at Kilclooney Stn., Qld, 18°50'S, 145°48'E.

PREVALENCE. Specimens recovered from 3 (19%) of 16 hosts examined.

***Macropodinium yalanbense* Dehority, 1996**
(Figs 9, 10D; Table 5)

MATERIAL. Voucher specimens from the eastern-grey kangaroo, Shaw, 1790: QMG463145, St. George, Qld, 28°01'S, 148°35'E; the western-grey kangaroo, *Macropus fuliginosus melanops* (Desmarest, 1817), QMG463146, Collie, WA, 33°21'S, 116°09'E; the common wallaroo, *Macropus robustus* Gould, 1841 (subspecies unknown), QMG463147, Brisbane, Qld, 27°28'S, 153°01'E; and the red-necked wallaby, *Macropus rufogriseus* (Desmarest, 1817), QMG463148, Brisbane, Qld, 27°28'S, 153°01'E.

DIFFERENTIAL DIAGNOSIS. *Ma. yalanbense* was the first *Macropodinium* species described which lacked both DB and VB; all previously described species possessed either or both features.

DESCRIPTION. Body oval to slightly reniform; 40.8–77.6 (58.4)µm long, 19.2–37.6 (28.2)µm deep, shape index (L/D) 1.5–2.9 (2.1); right side abbreviated compared to left side. Single macronucleus, spherical to ovoid; 6.4–16.8 (10.6)µm long by 4.8–14.4 (7.2)µm wide; located ventral to vestibulum. Single micronucleus, spherical to ovoid; 1.6–5.6 (2.9)µm long by 1.6–4.8 (2.3)µm wide; adjacent to the macronucleus. Vestibulum bent conical; 6.4–20.8 (13.3)µm wide by 11.2–24.8 (17.5)µm deep; opening subapically, directed anterioventrally. Somatic ciliation 4.8–9.6 (6.9)µm long; adoral cilia 4.8–8.8 (6.5)µm long. Pellicular diamond pattern uniform; left side bears 8–12 (10.6) longitudinal grooves; right side bears 8–12 (10.1) longitudinal grooves; longitudinal grooves 2.4–4.0 (3.1)µm apart. DVG shallow dorsally and ventrally. DB and VB absent. Ornamentations absent. Cytoproct slot-shaped; 1.6–4.0 (2.7)µm deep; opening posterior.

REMARKS. This species is also found in the western grey kangaroo, *Macropus fuliginosus*

TABLE 5. Morphometric characterisation of the macropodiniid ciliate, *Macropodinium yalanbense* Dehority, 1996, recovered from the eastern and western grey kangaroos, *Macropus giganteus* and *Macropus fuliginosus*; x: mean; SD: standard deviation; CV: coefficient of variation; min: minimum; max: maximum; n: number of observations.

Character	x	SD	CV	min	max	n
Body dimensions						
Length, L	58.4	7.85	13.5	40.8	77.6	140
Width, W	28.2	3.35	11.9	19.2	37.6	140
Shape index (L/W ratio)	2.1	0.29	14.1	1.5	2.9	140
Macronucleus						
Length	10.6	1.91	18.0	6.4	16.8	140
Width	7.2	1.29	18.0	4.8	14.4	140
Micronucleus						
Length	2.9	0.63	21.8	1.6	5.6	76
Width	2.3	0.59	26.1	1.6	4.8	76
Oral apparatus						
Vestibulum width	13.3	2.59	19.5	6.4	20.8	140
Vestibulum depth	17.5	2.81	16.0	11.2	24.8	138
Cytostome width	2.7	0.44	16.4	1.6	3.2	138
Length of oral cilia	6.5	0.88	13.6	4.8	8.8	96
Somatic ciliature						
Length of somatic cilia	6.9	0.92	13.3	4.8	9.6	107
Miscellaneous						
No Longitudinal grooves, Left side	10.6	0.65	6.1	8	12	134
No Longitudinal grooves, Right side	10.1	0.93	9.2	8	12	137
Width between longitudinal grooves	3.1	0.37	11.7	2.4	4.0	139
Cytoproct length	2.7	0.46	17.1	1.6	4.0	139

melanops (Desmarest, 1817) from Collie, WA 33°21'S, 116°09'E and Port Augusta, SA, 32°30'S, 137°46'E; the Kangaroo Is. kangaroo, *Macropus fuliginosus fuliginosus* (Desmarest, 1817) from Penneshaw, SA, 35°43'S, 137°56'E; the eastern-grey kangaroo, *Macropus giganteus*, Shaw, 1790 from Bendigo, Vic, 36°45'S, 144°16'E and Wee Jasper, NSW, 35°07'S, 148°40'E.

PREVALENCE. Specimens recovered from 6 (29%) of 21 western-grey kangaroos, 3 (60%) of 5 Kangaroo Is kangaroos, 11 (26%) of 43 eastern-grey kangaroos, 4 (11%) of 36 wallaroos and 1 (3%) of 32 red-necked wallabies examined.

***Macropodinium hallae* sp. nov.**
(Figs 11, 17A; Table 6)

ETYMOLOGY. For our colleague and helminthologist, Kathryn Hall.

MATERIAL. HOLOTYPE QMG463143, from the tammar wallaby, *Macropus eugenii* (Desmarest, 1817), Penneshaw, SA, 35°43'S, 137°56'E.

DIFFERENTIAL DIAGNOSIS. Five other *Macropodinium* species have prominent DB and VB, namely *marai*, *baldense*, *setonixium*, *moiri* and *bicolor*. *Ma. hallae* sp. nov. can be readily distinguished from the former three species on the basis of size

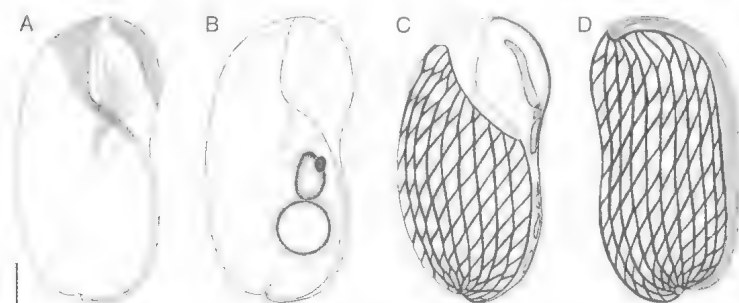


FIG. 9. Morphology and infraciliature of *Macropodinium yalanbense* Dehority, 1996. A, infraciliature. B, internal morphology. C, right view, surface features. D, left view, surface features. Scale bar = 10µm.

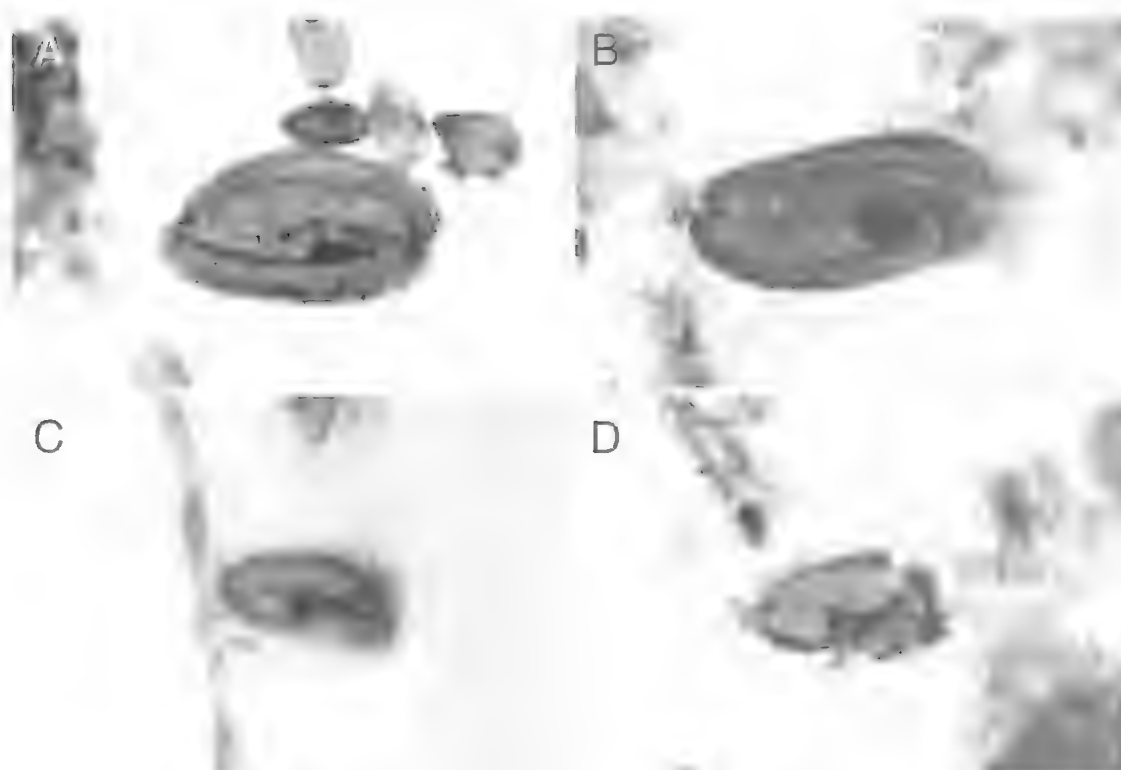


FIG. 10. Light micrographs of *Macropodinium* spp. A, *Ma. moiri*. B, *Ma. setonixium*. C, *Ma. emuensis*. D, *Ma. yalanhense*. Scale bars = 10 μ m.

and shape; all are small, oval species whereas *Ma. hallae* sp. nov. is a large, oval to oblong shaped species. *Ma. hallae* sp. nov. can be distinguished from *Ma. moiri* by the ornamentation (strongly crenulate right dorsal margin vs weakly flange-like right dorsal margin) and pellicular windows (entirely absent vs well-developed in the DVG). *Ma. hallae* sp. nov. can be distinguished from *Ma. bicolor* on the shape (oval vs broad with a prominent tail) and ornamentation (crenulate vs spine-like).

DESCRIPTION. Body oval to reniform; 53.6-79.2 (63.3) μ m long, 25.6-39.2 (33.4) μ m deep, shape index (L/D) 1.7-2.1 (1.9); right side slightly abbreviated compared with left side. Single macronucleus, oval to globotriangular; 8.8-14.4 (12.3) μ m long by 5.6-12.0 (7.8) μ m wide; located ventral to the vestibulum. Single micronucleus, oval to round;

2.4-4.0 (2.7) μ m long by 1.6-2.4 (2.2) μ m wide; generally adjacent to the macronucleus. Vestibulum funnel-like; 10.4-15.2 (12.4) μ m wide by 16.0-23.2 (19.8) μ m deep; opening subapically, directed anteroventrally. Cytopharynx composed of short rods issue directly from cytostome. Somatic ciliation 5.6-8.8 (6.9) μ m long; adoral cilia 4.8-8.8 (6.2) μ m long. Pellicular diamond pattern uniform; left side bears 8-10 (9.2) longitudinal

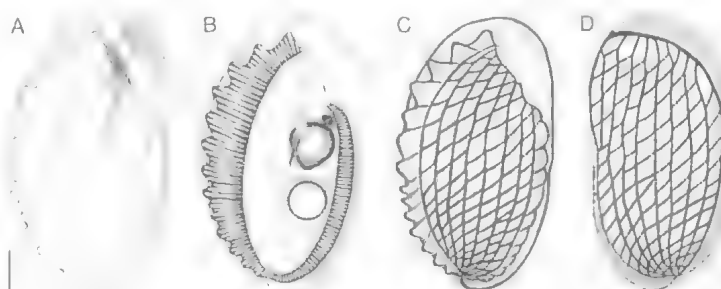


FIG. 11. Morphology and infraciliature of *Macropodinium hallae* sp. nov. A, infraciliature. B, internal morphology. C, right view, surface features. D, left view, surface features. Scale bar = 10 μ m.

TABLE 6. Morphometric characterisation of the macropodiniid ciliate, *Macropodinium hallae* sp. nov. recovered from the tammar wallaby, *Macropus eugenii*; x: mean; SD: standard deviation; CV: coefficient of variation; min: minimum; max: maximum; n: number of observations.

Character	x	SD	CV	min	max	n
Body dimensions						
Length, L	63.3	7.65	12.1	53.6	79.2	20
Width, W	33.4	3.98	11.9	25.6	39.2	20
Shape index (L/W ratio)	1.9	0.13	6.6	1.7	2.1	20
Macronucleus						
Length	12.3	1.61	13.1	8.8	14.4	20
Width	7.8	1.58	20.4	5.6	12.0	20
Micronucleus						
Length	2.7	0.63	23.0	2.4	4.0	7
Width	2.2	0.39	18.0	1.6	2.4	7
Oral apparatus						
Vestibulum width	12.4	1.43	11.6	10.4	15.2	20
Vestibulum depth	19.8	1.91	9.7	16.0	23.2	20
Cytostome width	1.6	0.32	19.2	0.8	2.4	20
Length of oral cilia	6.2	1.00	16.3	4.8	8.8	16
Somatic ciliation						
Length of somatic cilia	6.9	0.83	12.0	5.6	8.8	18
Miscellaneous						
No Longitudinal grooves, Left side	9.2	0.66	7.2	8	10	17
No Longitudinal grooves, Right side	7.8	0.58	7.5	7	9	16
Width between longitudinal grooves	3.4	0.44	12.9	2.4	4.0	19
Depth DB	8.6	1.18	13.7	5.6	9.6	10
Depth VB	3.8	1.09	28.9	2.4	6.4	19
Cytoproct length	3.3	0.73	22.2	2.4	4.8	20

grooves; right side bears 7-9 (7.8) longitudinal grooves; longitudinal grooves 2.4-4.0 (3.4) μ m apart. DVG deep dorsally and ventrally. DB prominent 5.6-9.6 (8.6) μ m deep; VB prominent 2.4-6.4 (3.8) μ m deep. Crenulate ornamentations right dorsal, flange ornamentations right ventral. Cytoproct slot-shaped; 2.4-4.8 (3.3) μ m deep; opening left.

PREVALENCE. Specimens recovered from 2 (14%) of 14 hosts examined.

***Macropodinium ocallaghani* sp. nov.**
(Figs 12, 13, 17C; Table 7)

ETYMOLOGY. For Michael O'Callaghan who, apart from considerable contributions to wildlife parasitology, also helped to recover this species.

MATERIAL. HOLOTYPE QMG463144, from the tammar wallaby, *Macropus eugenii* (Desmarest, 1817), Penneshaw, SA, 35°43'S, 137°56'E.

DIFFERENTIAL DIAGNOSIS. Aside from *Ma. ocallaghani* sp. nov., only *Ma. yalanbense* lacks both DB and VB. *Ma. ocallaghani* sp. nov. can be

distinguished from *Ma. yalanbense* by the structure of the oral aperture which is limited by the dorsal DVG in the former species but not in the latter species.

DESCRIPTION. Body reniform; 38.4-72.8 (56.5) μ m long, 20.8-33.6 (26.1) μ m deep, shape index (L/D) 1.5-3.0 (2.2); right side abbreviated compared with left side. Single macronucleus, oval to globotriangular; 5.6-16.0 (10.6) μ m long by 4.8-9.6 (7.1) μ m wide; located ventral to the vestibulum. Single micronucleus, oval to round; 1.6-3.2 (2.2) μ m long by 0.8-2.4 (1.7) μ m wide; generally adjacent to the macronucleus. Vestibulum bent conical; 10.4-16.0 (12.6) μ m wide by 16.0-25.6 (20.2) μ m deep; opening subapically, directed anteroventrally. Somatic ciliation 4.0-8.8 (6.7) μ m long; adoral cilia 3.2-8.0 (6.7) μ m long. Pellicular diamond pattern uniform; left side bears 7-11 (9.6) longitudinal grooves; right side bears 7-12 (8.5) longitudinal grooves; longitudinal grooves 2.4-4.0 (3.0) μ m apart. DVG shallow dorsally and ventrally; pellicular windows on DVG anterior and dorsal

TABLE 7. Morphometric characterisation of the macropodiniid ciliate, *Macropodinium ocallaghani* sp. nov. recovered from the tammar wallaby, *Macropus eugenii*; x: mean; SD: standard deviation; CV: coefficient of variation; min: minimum; max: maximum; n: number of observations.

Character	x	SD	CV	min	max	n
Body dimensions						
Length, L	56.5	6.90	12.2	38.4	72.8	70
Width, W	26.1	2.83	10.9	20.8	33.6	70
Shape index (L/W ratio)	2.2	0.25	11.5	1.5	3.0	70
Macronucleus						
Length	10.6	2.15	20.4	5.6	16.0	70
Width	7.1	1.12	15.8	4.8	9.6	70
Micronucleus						
Length	2.2	0.43	19.5	1.6	3.2	36
Width	1.7	0.36	20.6	0.8	2.4	36
Oral apparatus						
Vestibulum width	12.6	1.46	11.6	10.4	16.0	70
Vestibulum depth	20.2	2.08	10.3	16.0	25.6	70
Cytostome width	1.7	0.31	18.3	0.8	2.4	70
Length of oral cilia	5.7	1.17	20.6	3.2	8.0	60
Somatic ciliature						
Length of somatic cilia	6.7	1.01	15.1	4.0	8.8	66
Miscellaneous						
No Longitudinal grooves, Left side	9.6	0.85	8.8	7	11	58
No Longitudinal grooves, Right side	8.5	1.11	13.0	7	12	58
Width between longitudinal grooves	3.0	0.41	14.0	2.4	4.0	69
Cytoproct length	3.3	1.19	35.9	2.4	8.0	66

left side; DB and VB absent. Cell ornamentations absent. Cytoproct slot-shaped; 2.4–8.0 (3.3)µm deep; opening posterior.

REMARKS. This species also recovered from *Macropus eugenii* from Kangaroo Is., SA, 35°46'S, 137°37'E.

PREVALENCE. Specimens recovered from 12 (86%) of 14 hosts examined.

***Macropodinium petrogale* sp. nov.**
(Figs 14, 15, 17C; Table 8)

ETYMOLOGY. For the generic name of its rock-wallaby host.

MATERIAL. HOLOTYPE QMG463140, from Godman's rock-wallaby, *Petrogale godmani* Thomas, 1923, Church Hill, Curraghmore Stn., Qld, 16°27'S, 145°11'E.

DIFFERENTIAL DIAGNOSIS. Aside from *Ma. petrogale* sp. nov., only *Ma. tricresta* and *Ma. spinosus* possess a DB but lack a VB. *Ma. petrogale* sp. nov. can be readily distinguished from both by the absence of ornamentations which are prominent in both *tricresta* and *spinosus*.

DESCRIPTION. Body truncated elliptical, narrowing posteriorly; modest antero-leftward bend; 36.0–52.0 (44.3)µm long by 19.2–30.4 (24.7)µm deep, shape index

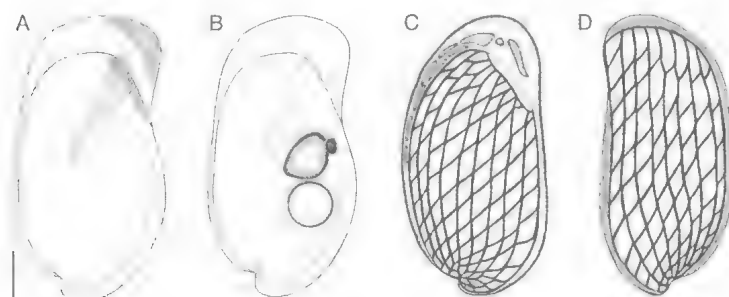


FIG. 12. Morphology and infraciliature of *Macropodinium ocallaghani* sp. nov. A, infraciliature. B, internal morphology. C, right view, surface features. D, left view, surface features. Scale bar = 10µm.

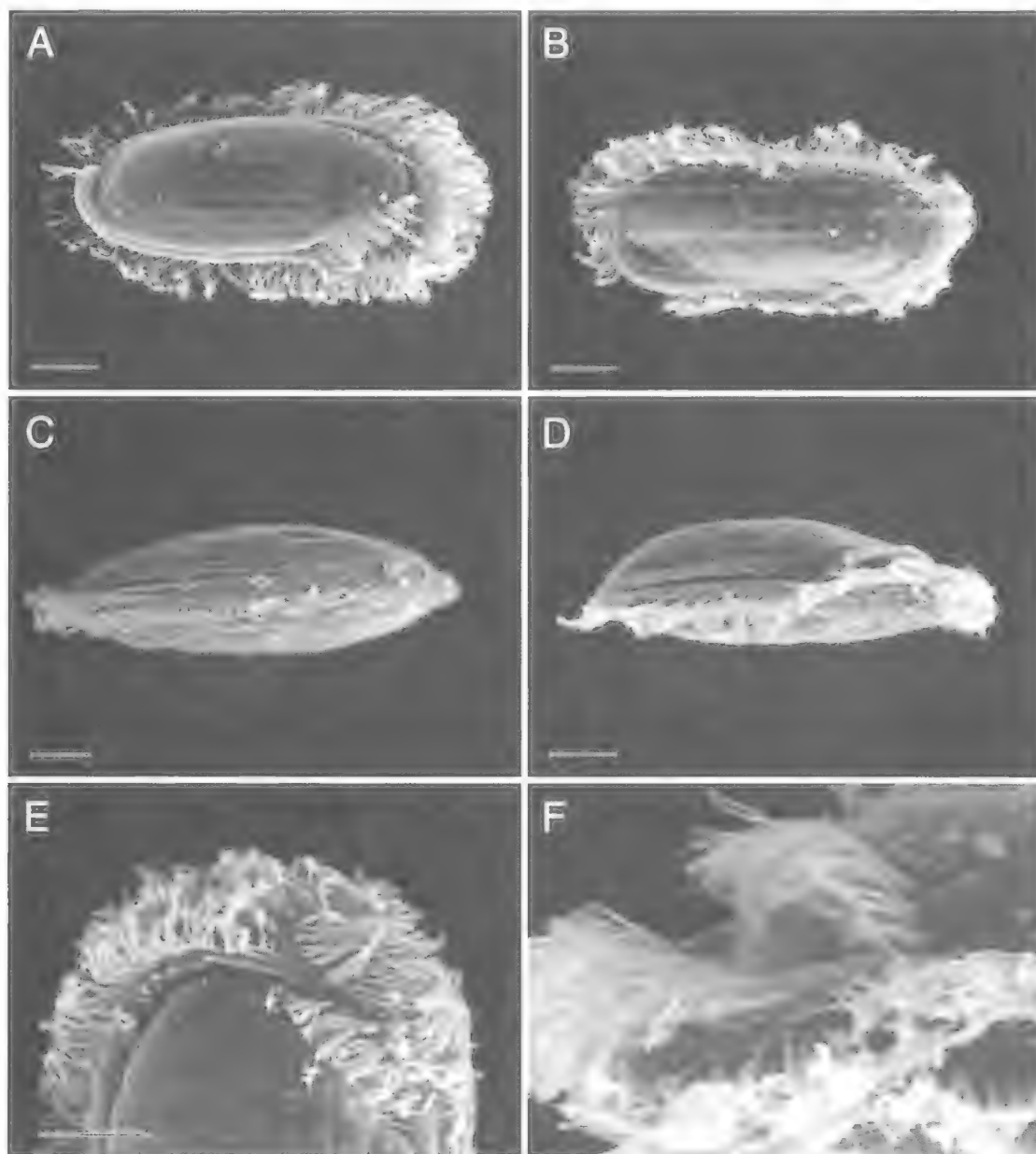


FIG 13. Scanning electron micrographs of *Macropodinium ocallaghani* sp. nov. A, right view, scale bar = 10µm. B, left view, scale bar = 10µm. C, dorsal view, scale bar = 10µm. D, ventral view, scale bar = 1µm. E, anterior right view, scale bar = 1µm. F, anterior dorsal view, scale bar = 1µm.

(L/D) 1.4-2.4 (1.8); right side only slightly abbreviated compared with left side. Single macronucleus spherical to globo-triangular; 6.4-10.4 (8.2)µm long by 4.0-7.2 (5.6)µm wide; located ventral to the vestibulum. Single micronucleus spherical to ovoid; 1.6-2.4 (2.1)µm long by 1.6-2.4 (1.7)µm wide, adjacent to or

obscured by the macronucleus. Vestibulum bent conical; 9.6-14.4 (12.2)µm wide by 11.2-21.6 (18.0)µm deep; opening apical, directed anteroventrally; cytostome 0.8-2.4 (1.7)µm wide. Somatic cilia 3.2-7.2 (4.5)µm long; adoral cilia 3.2-7.2 (4.4)µm long. Pellicular diamond pattern uniform; left side bears 9-11 (9.9)

TABLE 8. Morphometric characterisation of the macropodiniid ciliate, *Macropodinium petrogale* sp. nov. recovered from Godman's rock-wallaby, *Petrogale godmani*; x: mean; SD: standard deviation; CV: coefficient of variation; min: minimum; max: maximum; n: number of observations.

Character	x	SD	CV	min	max	n
Body dimensions						
Length, L	44.3	4.51	10.2	36.0	52.0	30
Width, W	24.7	2.83	11.5	19.2	30.4	30
Shape index (L/W ratio)	1.8	0.20	11.0	1.4	2.4	30
Macronucleus						
Length	8.2	1.18	14.4	6.4	10.4	30
Width	5.6	0.85	15.3	4.0	7.2	30
Micronucleus						
Length	2.1	0.41	12.0	1.6	2.4	14
Width	1.7	0.29	17.0	1.6	2.4	14
Oral apparatus						
Vestibulum width	12.2	1.34	11.0	9.6	14.4	30
Vestibulum depth	18.0	2.37	13.2	11.2	21.6	30
Cytostome width	1.7	0.38	22.9	0.8	2.4	30
Length of oral cilia	4.4	0.21	24.6	3.2	7.2	26
Somatic ciliature						
Length of somatic cilia	4.5	1.09	24.2	3.2	7.2	28
Miscellaneous						
No Longitudinal grooves, Left side	9.9	0.58	5.9	9	11	30
No Longitudinal grooves, Right side	8.0	0.56	6.9	7	9	30
Width between longitudinal grooves	3.2	0.59	18.5	2.4	4.0	12
Depth DB	4.0	0.65	16.1	2.4	4.8	30
Cytoproct length	3.0	0.53	17.5	2.4	4.0	30

longitudinal grooves, right side bears 7-9 (8.0) longitudinal grooves; longitudinal grooves 2.4-4.0 (3.2) μm apart. DVG shallow dorsally and ventrally. DB prominent 2.4-4.8 (4.0) μm deep. VB absent. Ornamentations absent. Cytoproct cup-shaped; 2.4-4.0 (3.0) μm deep; opening posterior.

PREVALENCE. Specimens recovered from 3 (100%) of 3 hosts examined.

Macropodinium titan sp. nov.

(Figs 16, 17D; Table 9)

ETYMOLOGY. For its great size and robust shape.

MATERIAL. HOLOTYPE QMG463151, from Godman's rock-wallaby, *Petrogale godmani* Thomas, 1923, Church Hill, Curraghmore Stn, Qld, 16°27'S, 145°11'E.

DIFFERENTIAL DIAGNOSIS. The only other *Macropodinium* species which possesses a VB

but lacks a DB is *Ma. ennuensis* (both forms). *Ma. titan* sp. nov. and *Ma. ennuensis* can be readily distinguished on size (the former is much larger), shape (the former is oval, the latter reniform), cell curvature (the right side envelops the left side in the former species whereas it does not in the latter), host occurrence (rock-wallaby vs wallaroo) and absence of the non-patterned strip on the left surface of *Ma. ennuensis*.

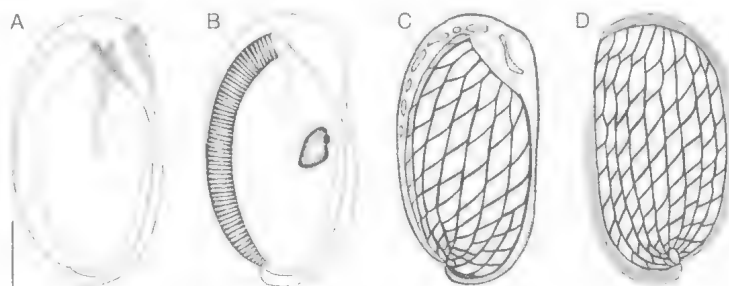


FIG. 14. Morphology and infraciliature of *Macropodinium petrogale* sp. nov. A, infraciliature. B, internal morphology. C, right view, surface features. D, left view, surface features. Scale bar = 10 μm .

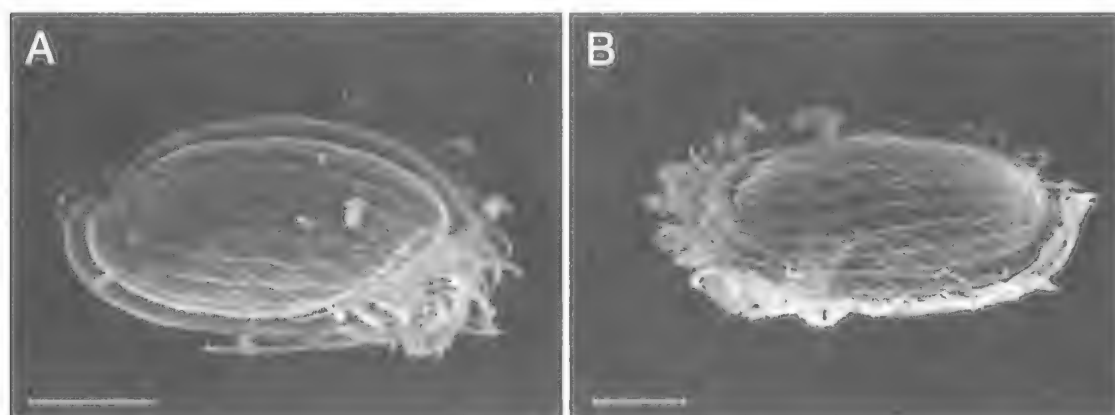


FIG. 15. Scanning electron micrographs of *Macropodinium petrogale* sp. nov. A, right view. B, left view. Scale bars = 10µm.

TABLE 9. Morphometric characterisation of the macropodiniid ciliate, *Macropodinium titan* sp. nov. recovered from Godman's rock-wallaby, *Petrogale godmani*; x: mean; SD: standard deviation; CV: coefficient of variation; min: minimum; max: maximum; n: number of observations.

Character	x	SD	CV	min	max	n
Body dimensions						
Length, L	88.1	10.10	11.5	64.8	104.0	13
Width, W	60.4	3.57	5.9	52.8	64.0	13
Shape index (L/W ratio)	1.5	0.16	10.7	1.2	1.7	13
Macronucleus						
Length	15.7	2.86	18.2	11.2	21.6	13
Width	11.0	1.05	9.6	9.6	12.8	13
Micronucleus						
Length	6.2	1.32	21.5	4.8	8.8	13
Width	5.0	0.87	17.5	4.0	7.2	13
Oral apparatus						
Vestibulum width	22.7	3.26	14.4	15.2	26.4	13
Vestibulum depth	36.5	5.15	14.1	28.8	44.0	13
Cytostome width	2.6	0.38	14.5	2.4	3.2	13
Length of oral cilia	5.5	1.49	27.2	3.2	8.8	13
Somatic ciliature						
Length of somatic cilia	5.4	1.00	18.7	4.0	7.2	10
Miscellaneous						
No Longitudinal grooves, Left side	11.7	0.95	8.1	10	13	13
No Longitudinal grooves, Right side	19.7	1.32	6.7	18	22	13
Width between longitudinal grooves, Left side	3.7	0.46	12.4	3.2	4.0	3
Width between longitudinal grooves, Right side	2.4	0.80	33.3	1.6	3.2	3
Depth VB	13.8	1.57	11.4	11.2	16.0	13
Width non-patterned stripe	9.9	1.29	13.0	8.0	12.8	13
Cytoproct length	5.9	0.70	11.8	4.8	7.2	13

DESCRIPTION. Body ovoid; 64.8-104.0 (88.1)µm long by 52.8-64.0 (60.4)µm deep, shape index (L/D) 1.2-1.7 (1.5); right side not abbreviated compared to left side. Single

macronucleus ovoid to pyriform; 11.2-21.6 (15.7)µm long by 9.6-12.8 (11.0)µm wide; located ventral to vestibulum. Single micronucleus spherical to ovoid; 4.8-8.8 (6.2)µm

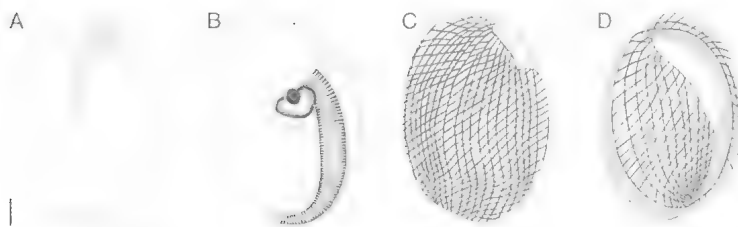


FIG. 16. Morphology and infraciliature of *Macropodinium titan* sp. nov. A, infraciliature. B, internal morphology. C, right view, surface features. D, left view, surface features. Scale bar = 10µm.

longitudinal grooves 3.2-4.0 (3.7)µm apart; right-side longitudinal grooves 1.6-3.2 (2.4)µm apart. Right side envelops dorsal left side; left side convex, curving leftward ventrally. DVG deep ventrally. DB absent. VB prominent 8.0-12.8 (9.9)µm deep. Obvious unpatterned, non-ciliated strip separates left side patterning from dorsal somatic ciliary

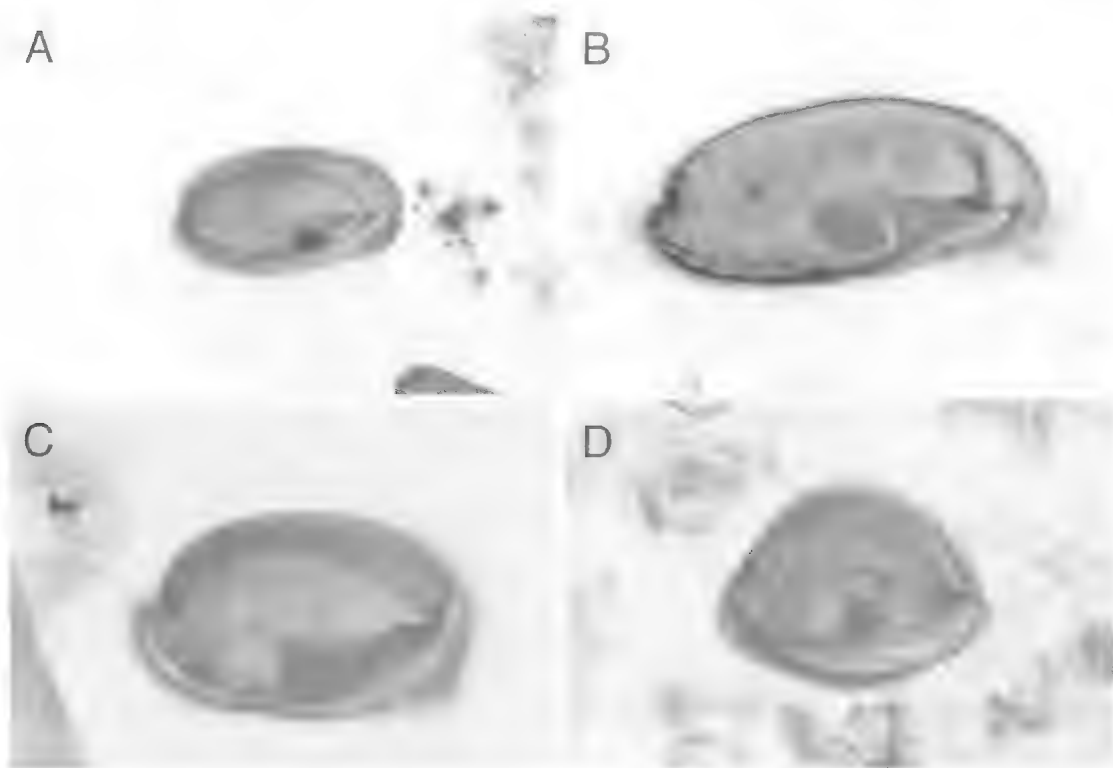


FIG. 17. Light micrographs of *Macropodinium* spp. A, *Ma. hallae*. B, *Ma. ocallaghani*. C, *Ma. petrogale*. D, *Ma. titan*. Scale bars = 10µm.

long by 4.0-7.2 (5.0)µm wide; adjacent to or obscured by macronucleus. Vestibulum bent conical; 15.2-26.4 (22.7)µm wide by 28.8-44.0 (36.5)µm deep; opening apical, directed anterioventrally, surrounded by prominent circumoral collar; cytostome 2.4-3.2 (2.6)µm wide. Somatic cilia 4.0-7.2 (5.4)µm long; adoral cilia 3.2-8.8 (5.5)µm long. Pellicular diamond pattern non-uniform; left side bears 10-13 (11.7) longitudinal grooves, right side bears 18-22 (19.7) longitudinal grooves; left-side

field. Ornamentations absent. Cytoproct slot-shaped; 4.8-7.2 (5.9)µm deep; opening posteriorly; ventral cytoproct spine present.

PREVALENCE. Specimens recovered from 2 (66%) of 3 hosts examined.

KEY TO THE SPECIES OF *MACROPODINIUM*

1. Prominent ventral and dorsal bars 2
- Prominent ventral bar, dorsal bar absent 6
- Prominent dorsal bar, ventral bar absent 7

TABLE 10. Comparison of morphometrics of *Macropodinium moiri* and *Ma. setonixium*.

	<i>Ma. moiri</i> Dehority (1996)	<i>Ma. moiri</i> Present study	<i>Ma. setonixium</i> Dehority (1996)	<i>Ma. setonixium</i> Present study
Length				
Range	65-127	60.8-100.8	24-50	24.8-46.4
X	85.2	81.0	38.0	32.1
SD	13.1	12.88	5.9	4.6
Width				
Range	41-73	32.8-48.8	18-40	15.2-24.8
X	54.8	40.8	27.9	18.8
SD	7.0	4.44	4.6	2.148
Shape index				
Range	1.2-2.0	1.4-2.3	1.0-1.6	1.3-2.1
X	1.56	2.0	1.37	1.7
SD	0.18	0.2	0.12	0.2

- Both dorsal and ventral bars absent 9
2. Prominent marginal ornamentations on at least one part of the cell 3
No ornamentations, at best slight marginal flange . . . 5
3. Pellicle plates in DVG left dorsal and right ventral *moiri*
Pellicle plates not wrapped into DVG 4
4. Cell oval with prominent tail; left cell half ornamented *bicolor*
Cell reniform without tail; right cell half ornamented *hallae*
Cell oval without prominent tail; right cell half ornamented *baldense*
5. Cell oval, small (<50µm long), no preoral kineties *setonixium*
Cells elongate, large (>60µm long), preoral kineties *moiri*
6. Cell small & reniform, prominent pellicular windows *ennuensis*
Cell large, oval and twisted left, lacks pellicular windows *titan*
7. Prominent cell ornamentations 8
No cell ornamentations, small oval ciliate *petrogale*
8. Cell wedge-shaped; ventral spines, dorsal flange *spinosus*
Cell broadly oval; ventral spines, dorsal crenulations; strong left bend; extracalary dorsal DVG *tricresta*
9. Prominent dorsal pellicular windows, limited mouth *ocallaghani*
Prominent ventral pellicular windows, entire mouth *yalanbense*

DISCUSSION

Macropodinium comprises the most diverse and distinctive component of the ciliate fauna of macropodid marsupials. Collectively (Cameron

TABLE 11. Comparison of morphometrics of *Ma. ennuensis*¹ and *Ma. yalanbense*. ¹*Ma. ennuensis* f. *ennuensis* as this was the form described by Dehority (1996).

	<i>Ma. ennuensis</i> Dehority (1996)	<i>Ma. ennuensis</i> Present study ¹	<i>Ma. yalanbense</i> Dehority (1996)	<i>Ma. yalanbense</i> Present study
Length				
Range	43-66	37.6-70.4	47-75	40.8-77.6
X	55.3	56.2	62.6	58.4
SD	4.6	6.9	6.9	7.85
Width				
Range	23-33	20.0-33.6	29-41	19.2-37.6
X	28.3	26.4	34.2	28.2
SD	2.6	3.10	2.7	3.35
Shape index				
Range	1.6-2.4	1.5-3.0	1.5-2.2	1.5-2.9
X	1.96	2.1	1.83	2.1
SD	0.16	0.23	0.14	0.29

et al. 2001; present study) we have described 12 species within the genus, including 4 redescrptions of species originally erected by Dehority (1996). Redescrptions were deemed necessary on the basis of staining techniques. Dehority (1996) used methylene blue, methyl green and haematoxylin which failed to resolve the fine differences between the three components of the oral ciliature of *Macropodinium* spp., namely the adoral, vestibular and preoral kinety bands. We used protargol and silver carbonate staining which produced finer resolution of the somatic kineties, dorsal and ventral bars and the pellicular windows. Comparisons of the morphometric descriptors published here and in Dehority (1996) (Tables 10, 11) show that they are broadly in agreement, although with a slight tendency towards the specimens recorded here being smaller. We are therefore confident that we have accurately redescrbed 4 of the species presented in Dehority (1996) to include the additional features of the genus first reported in Cameron et al. (2001), namely cell orientation, cell ornamentations and oral ciliation.

Intraspecific variation was examined in detail in *Ma. yalanbense* and *Ma. ennuensis* by examination of the morphometric differences between isolates from different host species and subspecies. *Ma. yalanbense* is the only *Macropodinium* species which has been recorded in more than one host species. It has been recovered from native populations of the eastern

TABLE 12. Comparative morphometrics of *Macropodinium yalanbense*, Dehority 1996, isolates from *Macropus giganteus*, *M. fuliginosus melanops* and *M. fuliginosus fuliginosus*; 'expressed as a range with the mean in parentheses.

Character	<i>M. giganteus</i>	<i>M. f. fuliginosus</i>	<i>M. f. melanops</i>
Body dimensions			
Length, L	40.8-77.6 (61.7)	45.6-63.2 (54.5)	43.2-69.6 (53.5)
Width, W	21.6-37.6 (28.0)	24.8-36.0 (29.3)	19.2-34.4 (27.5)
Shape index (L/W ratio)	1.7-2.9 (2.2)	1.7-2.1 (1.9)	1.5-2.7 (2.0)
Macronucleus			
Length	6.4-16.8 (11.1)	7.2-11.2 (9.3)	7.2-16.8 (10.5)
Width	4.8-10.4 (7.2)	4.8-10.4 (6.8)	4.8-14.4 (7.4)
Micronucleus			
Length	2.4-5.6 (3.0)	1.6-3.2 (2.5)	2.4-4.0 (2.6)
Width	1.6-4.8 (2.4)	1.6-2.4 (1.7)	1.6-3.2 (2.1)
Oral apparatus			
Vestibulum width	8.8-20.8 (14.3)	8.0-18.4 (12.6)	6.4-15.2 (11.3)
Vestibulum depth	11.2-24.8 (18.5)	13.6-22.4 (17.3)	11.2-19.2 (15.3)
Cytostome width	1.6-3.2 (2.7)	1.6-3.2 (2.6)	1.6-3.2 (2.6)
Oral ciliary length	4.8-8.8 (6.5)	4.8-8.8 (6.5)	4.8-7.2 (6.3)
Somatic ciliature			
Somatic ciliary length	4.8-9.6 (7.0)	5.6-8.8 (6.4)	6.4-8.8 (6.9)
Miscellaneous			
No Longitudinal grooves, Left side	8-12 (10.5)	10-12 (10.8)	10-12 (10.8)
No Longitudinal grooves, Right side	8-12 (10.1)	8-12 (9.7)	9-12 (10.6)
Width between longitudinal grooves	2.4-4.0 (3.2)	2.4-4.0 (3.2)	2.4-3.2 (2.9)
Cytoproct length	1.6-3.2 (2.6)	1.6-4.0 (2.7)	2.4-3.2 (2.7)

and western grey kangaroo (*M. giganteus* and *M. fuliginosus*) and captive populations of wallaroos (*M. robustus*) and red-necked wallabies (*M. rufogriseus*). The two native hosts are bigemminate species which diverged during the last ice age due to separation of a formerly widespread species to the eastern and southwestern fringes of the continent (Flannery, 1989). At the end of the ice age, the retreat of the central desert established favourable habitats across southern Australia and the two species now overlap in regions around the South Australian/New South Wales border (Strahan, 1996). No significant differences were found between isolates from the two subspecies of western grey kangaroos (*M. f. fuliginosus* and *M. f. melanops*) or between the two grey kangaroo species (Table 12). These hosts also share the amylovoracid ciliates *Amylovorax dehorityi* and *Bitricha obolata* (Cameron et al., 2000a). Finally, there have been no obvious local acquisitions of ciliates from sympatric macropodids. It is probable that the ciliate fauna found predates the split between the host species. As the habitat and diet of the host probably did

not change through the period of isolation (Flannery, 1989), it is possible that there was no selective pressure for differentiation in the ciliate species. Any speciation in the ciliates would therefore be the result of genetic drift rather than directional selection. There are three possible explanations for the observed pattern. First, the ciliates failed to diverge sufficiently due to random chance alone for speciation to result. Secondly, they may have speciated cryptically. Thirdly, one of the lineages of ciliates may have successfully displaced its bigemminate pair in the other host species once the kangaroos were again sympatric. Assessments of genetic variability in the ciliates across a wide geographic range, including the sympatric zone, would greatly contribute to our understanding of the parasite species flow within grey kangaroos.

In contrast, *Ma. ennuensis* which is associated with the wallaroo, *M. robustus*, appears to have differentiated more despite less host divergence. Consistent differences were found between ciliates from the two subspecies of host. *Ma. ennuensis* f. *dentis* from the eastern subspecies (*M. r. robustus*) has an oral spur and 2

more longitudinal grooves on the right cell side than *Ma. emmensis* f. *emmensis* from the western subspecies (*M. r. erubescens*). The divergence between the two forms is modest in comparison to the difference between other *Macropodinium* species, and for this reason they have not been erected as separate species. The biogeographic history and distribution of *M. robustus* is not as well understood as *M. giganteus*/*M. fuliginosus* but it is also believed to have been marginalised by ice age expansions of the central deserts of Australia. *M. robustus* is more serically adapted than either *M. giganteus* or *M. fuliginosus* and thus probably experienced less habitat contraction due to desert expansion (Strahan, 1995). This would explain the failure of the host to speciate but not the divergences within the ciliates. Assessments of the ciliate fauna of the northern wallaroo subspecies, *M. robustus woodwardi*, and the other wallaroo species, *M. antilopinus* and *M. bernadus*, and the genetic structure of their faunas would help explain the evolution of ciliate diversity within the wallaroos.

While most species of *Macropodinium* utilise only a single species of host, several host species harbour more than one species of *Macropodinium*. The quokka (*Setonix brachyurus*) had *Ma. moiri*, *Ma. setonixium* and *Ma. baldense* (Dehority, 1996), the black-striped wallaby (*M. dorsalis*) had *Ma. tricerata* and *Ma. spinosus* (Cameron et al., 2001), the tammar wallaby (*M. eugenii*) had *Ma. hallae* and *Ma. ocellaghani* (present paper) and Godman's rock-wallaby (*Petrogale godmani*) had *Ma. petrogale* and *Ma. titan* (present paper). These 4 hosts have little in common in terms of phylogenetic history or biogeographic distribution. All 4 are considered to be browsers. There are, however, species of browsing macropodids which are host to only a single *Macropodinium* species (*Thylogale billardieri* and *Wallabia bicolor*) (Cameron et al., 2001) or none at all (*M. agilis*, *M. parryi*, *M. rufogriseus*, *Petrogale assimilis*, *P. herberti* and *P. sharmani*). Therefore, simple dietary descriptors alone cannot explain this pattern.

The presence of multiple congeners in a single host species (and indeed single host animals) is common within the trichostome ciliates, and it appears that *Macropodinium* is no different. The reasons for this pattern of co-occurrence are unknown. Within the oplryoscolecids, which are associated with ruminants, multiple species of *Eutodinium* commonly occur in domesticated livestock. It has been proposed that this is due to

species which have host switched from non-domesticated ruminants such as deer or antelope accumulating over time and being spread globally by livestock trading (Williams & Coleman, 1991). Most macropodid species are sympatric with at most 2 other species, so opportunities for such profligate host switching are therefore less prevalent.

Macropodinium is the most diverse genus of ciliates in macropodid marsupials, in terms of both species diversity and structural complexity. The patterns of their host occurrence may, in some cases, be related to either biogeographic history or dietary preferences of their hosts. However, these conclusions are hampered by a lack of knowledge of phylogenetic relationships between both ciliates and their hosts. Such knowledge will greatly contribute to understanding how the Australian fauna of trichostome ciliates has evolved.

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LITERATURE CITED

- CAMERON, S.L. & O'DONOGHUE, P.J. in press. The ultrastructure of *Amylavorax dehorityi* comb. nov. and erection of the Amylavoracidae fam. nov. (Ciliophora: Trichostomatia). *European Journal of Protistology*.
- CAMERON, S.L., O'DONOGHUE, P.J. & ADLARD, R.D. 2000a. Novel isotrichid ciliates endosymbiotic in Australian macropodid marsupials. *Systematic Parasitology* 46: 45-57.
- 2000b. First record of *Cycloposthium edentatum* Strelkow, 1928 from the black-striped wallaby, *Macrophys dorsalis*. *Parasitology Research* 86: 158-162.
2001. Four new species of *Macropodinium* (Litostomatea: Macropodiniidae) from

- Australian wallabies and pademelons. *Journal of Eukaryotic Microbiology* 48:542-555.
- CORLISS, J.O. 1979. The ciliated Protozoa, characterisation, classification and guide to the literature. 2nd ed. (Pergamon Press: Oxford).
- DEHORITY, B.A. 1996. A new family of entodiniomorph protozoa from the marsupial forestomach, with descriptions of a new genus and five new species. *Journal of Eukaryotic Microbiology* 43: 285-295.
- DELLOW, D., HUME, I., CLARKE, R. & BAUCHOP, T. 1988. Microbial activities in the forestomach of free-living macropodid marsupials: comparisons with laboratory studies. *Australian Journal of Zoology* 36: 383-395.
- FOISSNER, W. 1991. Basic light and scanning electron microscopic methods for taxonomic studies of ciliated protozoa. *European Journal of Protistology* 27: 313-330.
- FLANNERY, T. 1989. Phylogeny of the Macropodoidea: a study in convergence. Pp. 1-46. In Grigg, G., Jarman, P. & Hume, I. (eds) *Kangaroos, Wallabies and Rat-Kangaroos*. Vol. 1. (Surrey Beatty and Sons: Chipping Norton).
- ITO, A. & IMAI, S. 1998. Infraciliary bands in the rumen ophryoscolecoid ciliate *Ostracodinium gracile* (Dogiel, 1925) observed by light microscopy. *Journal of Eukaryotic Microbiology* 45: 628-636.
- LINTERN-MOORE, S. 1973. Incorporation of dietary nitrogen into microbial nitrogen in the forestomach of the Kangaroo Island wallaby *Protemnodon eugenii* (Desmarest). *Comparative Biochemistry and Physiology* 44A: 75-82.
- LYNN, D.H. 1992. Protargol staining. Pp C4.1-C4.8. In Lee, J. & Soldo, A. (eds) *Protocols in protozoology*. (Society of Protozoologists: Lawrence).
- OBENDORF, D.L. 1984. The macropodid oesophagus IV. Observations on the protozoan fauna of the macropodid stomach and oesophagus. *Australian Journal of Biological Sciences* 37: 117-122.
- STRAHAN, R. 1995. *The mammals of Australia*. (New Holland Publishers: Sydney).
- WICKLOW, B.J. & HILL, B.F. 1992. A short procedure for protargol staining. Pp. C5.1-C5.4. In Lee, J. & Soldo, A. (eds) *Protocols in protozoology* (Society of Protozoologists: Lawrence).
- WILLIAMS, A. & COLEMAN, G. 1991. *The Rumen Protozoa*. (Springer-Verlag: New York).

A NEW DEVONIAN FERN, *FANNINGOPTERIS WYATTII*, FROM QUEENSLAND

H. TREVOR CLIFFORD

Clifford, H.T. 2002 5 31: A new Devonian fern, *Fanningopteris wyattii*, from Queensland. *Memoirs of the Queensland Museum* 48(1): 71-77. Brisbane. ISSN 0079-8835.

A new fern, *Fanningopteris wyattii* gen. et sp. nov., is described from late Givetian sediments in the Cultivation Gully Formation, Burdekin Basin, northeast Queensland. □ *Fanningopteris*, *Stauropteridales*, fern, Devonian, Givetian.

H.T.Clifford, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 19 February 1999.

The discovery, at Cultivation Gully about 70k southwest of Townsville, of a small silicified float containing numerous, anatomically similar, permineralised fossil fern axes (Fig.1) is noteworthy for the sediments are late Givetian thereby extending by several million years the known history of pteridophytes in Australia. Previously the oldest known Australian fossil fern was portion of a false-stem of *Austroclepsis australis* (Osborn) Sahni collected from rocks of Frasnian or Famennian age in the bed of the Manilla River about 20k west of Barabba, NSW (Osborn, 1916; Sahni, 1928).

STRATIGRAPHY

The Cultivation Gully Formation in the Burdekin Basin of the Townsville hinterland consists of a series of paralic lithofelspathic sandstones, mudstones, siltstones and tuffs whose basal member was deposited in a marine environment. The specimen was collected as a float from immediately above these sediments which have been assigned a late Givetian age (380.8-377.4 Ma Harland et al., 1990) on the basis of conodonts and coral assemblages (Talent & Mawson, 1994). As the silicified float was extracted from marine sediments it must have been reworked from elsewhere and so the fern axes may be somewhat older than the age here assigned them.

Fragmentary plant remains occur throughout the Formation (Cook et al., 1994) but, other than a lycopod which has been assigned tentatively to *Schizopodium* (Henderson & Crosdale, 1998), none has been identified. Unlike the fern axes these plants are preserved as coalified impressions in siltstone.

SYSTEMATIC PALAEOONTOLOGY

Division PTERIDOPHYTA
Order STAUROPTERIDALES
***Fanningopteris* gen. nov.**

ETYMOLOGY. Greek, *ptēris*, a kind of fern; Fanning River, type locality.

DIAGNOSIS. Erect, dichotomously branched rhizomatous herb with adventitious roots; all axes more or less cylindrical and anatomically similar; vascular tissue a single centrally placed cylindrical exarch protostele; in transverse section xylem strand mostly quadrangular but sometimes triangular in outline; tracheid elements indirectly attached annular or indirectly attached tilted annular; phloem alternating with protoxylem poles; pericycle narrow; endodermis a single row of rectangular cells; cortex differentiated into a narrow outer zone of thick-walled cells and a broad inner zone of thin-walled cells; sporophylls, sporangia and spores not known (Fig. 2).

***Fanningopteris wyattii* sp. nov.**
(Figs 1-6)

ETYMOLOGY. For D.H.Wyatt, for substantial contributions to the geology of North Queensland.

MATERIAL. Holotype. QMF 40510 from 70k southwest of Townsville at 19°43'S, 146° 27'E, coll. A.G. Cook.

DESCRIPTION. An erect, rhizomatous, glabrous, dichotomously branched herb; all axes anatomically similar, 1.4-4.7mm in diameter, intertwining, more or less circular in transverse section, with the perimeter interrupted by a series of low triangular projections representing vertically oriented ridges or non-vascularised enations, rarely expanded to form wings (Fig. 2); vasculature a centrally placed, circular protostele (Fig. 3), but sometimes with two steles

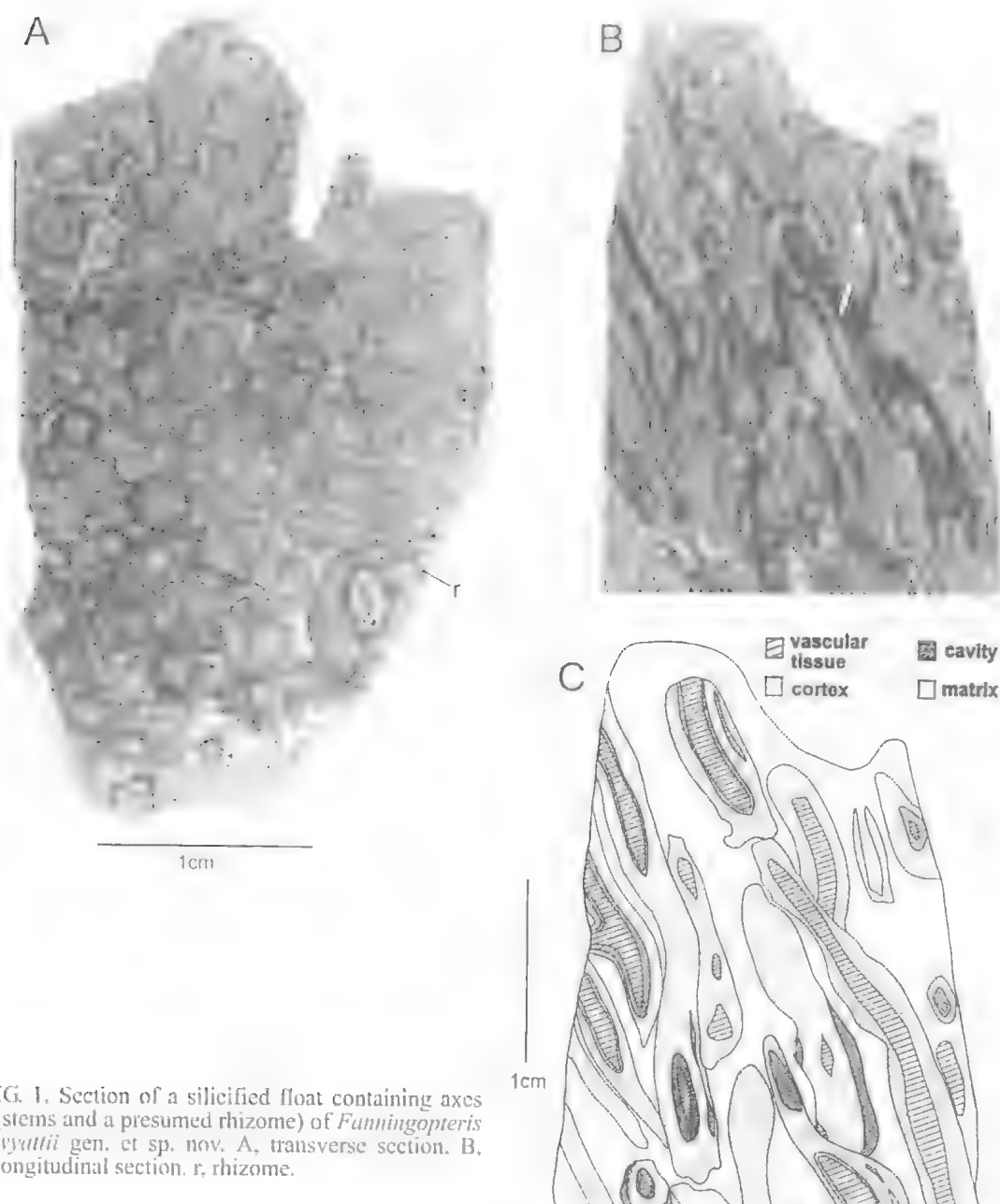


FIG. 1. Section of a silicified float containing axes (stems and a presumed rhizome) of *Funningopteris wyattii* gen. et sp. nov. A, transverse section. B, longitudinal section. r, rhizome.

immediately below a dichotomy (Fig. 2); xylem strand quadrangular or rarely triangular (Fig. 2), with sides somewhat concave between the protoxylem poles; metaxylem tracheid elements mostly 120-140 μ m in diameter and distributed evenly throughout the tissue; protoxylem tracheid elements with diameters of 4-8 microns; phloem occupying lens-shaped areas and alternating with the protoxylem poles, presumed

sieve tubes (Fig. 3) about 40 μ m in diameter intermixed with parenchyma cells 16-20 μ m in diameter; pericycle one to a few cells wide; endodermis of rectangular parenchymatous cells (Fig. 3) with a tangential length of about 64 microns and a radial width of about 42 μ m; Casparian strip not evident (Fig. 3); cortex differentiated into two zones, a narrow outer

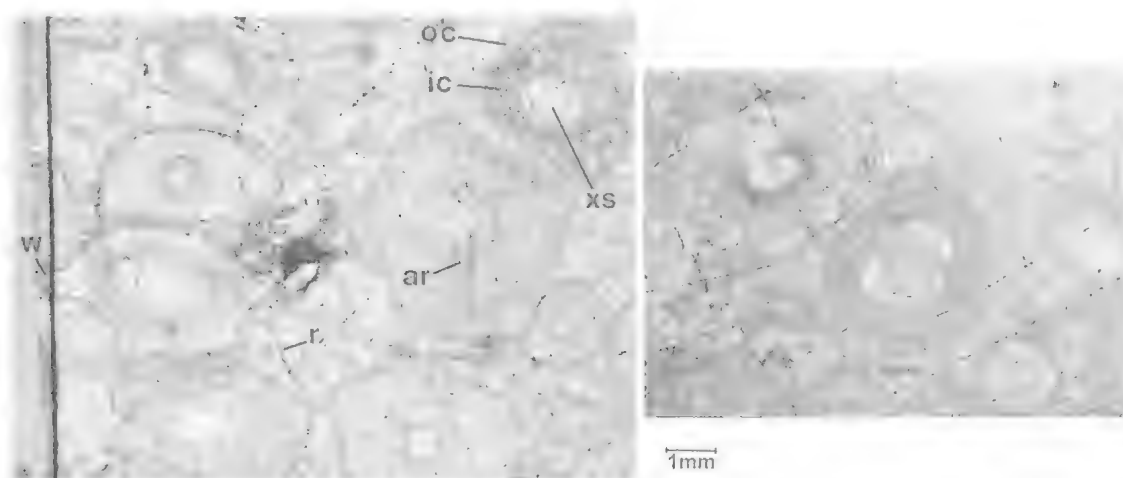


FIG. 2. Axes of *Fanningopteris wyattii* gen. et sp. nov. in transverse section. ar, adventitious root; ic, inner cortex; oc, outer cortex; r, rib; w, wing; xs, xylem strand. Note large stem with two xylem strands.

band, about four cells wide, of rectangular tangentially elongated thick-walled cells ($60 \times 20 \mu\text{m}$) and a broad inner band, 6-16 cells in width of isodiametric parenchymatous cells varying from $112-32 \mu\text{m}$ in diameter (Fig. 4A-B); airspaces lacking throughout the cortex and xylem; rhizomes up to 5.4mm in diameter and anatomically similar to axes but differing in that the cortex is not markedly differentiated into two zones (Fig. 1A); adventitious roots about 0.5mm in diameter; sporophylls, sporangia and spores not known.

In vertical section the xylem is seen to be composed entirely of annular, tilted annular or indirectly attached annular tracheid elements as

defined by Bierhorst (1960). The spacing of the annuli is independent of the diameter of the tracheid element in which they are formed and so aside from cell diameter there is no distinction between the meta- and protoxylem tissue.

The tracheid elements which resemble those of the zosterophyll *Gosslingia breconensis* (Kenrick & Edwards, 1988; Kenrick & Crane, 1997) are strengthened by the deposition on their primary walls of annuli of unknown chemical composition. The annuli vary in height from $10-12 \mu\text{m}$ and in width from $8.0-4.8 \mu\text{m}$. As seen in section the annuli expand abruptly from the primary cell wall to a maximum width and thereafter taper to an obtuse apex (Fig. 4C). In

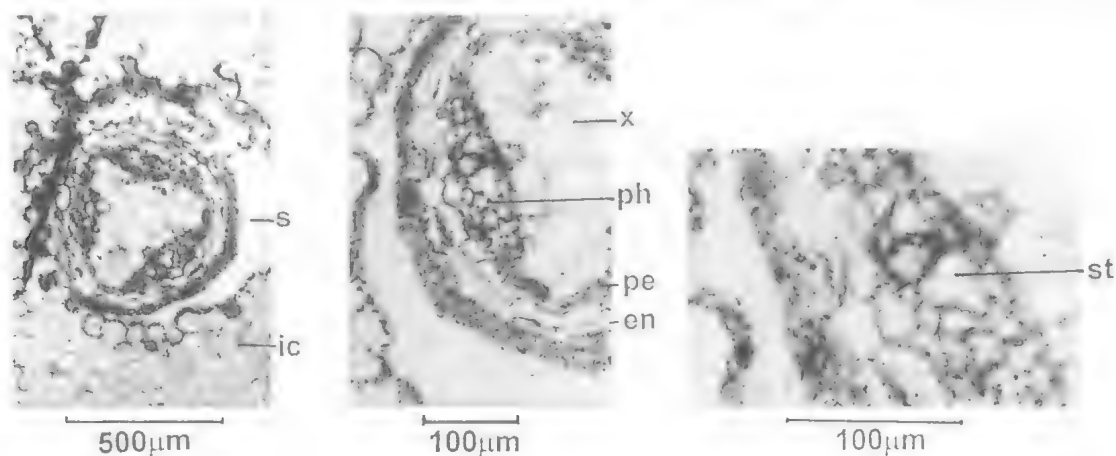


FIG. 3. Stelar anatomy of *Fanningopteris wyattii* gen. et sp. nov. in transverse section. e, endodermis; ic, inner cortex; p, pericycle; ph, phloem; st, sieve tube; xs, xylem strand.

most tracheid elements the annuli are destroyed during the process of fossilisation. However, their former presence is indicated by thin strands of magnetite which have been deposited on the primary cell walls between the bases of adjacent annuli (Fig. 5A). The strands sometimes divide (Fig. 4C,5A) which has been taken as evidence for some of the annuli being indirectly attached. None of the strands has been observed to assume the form of a spiral. The end walls of the tracheid elements are transverse or tapering (Fig. 5C) in which respect they are similar to the cells of the inner cortex (Fig. 5B). The cells of the xylem and inner cortex are mostly much longer than broad. However, due to the flexuous habit of the stems in the sections available both end walls are seen in only the shortest cells. Therefore it has not been possible to estimate the mean lengths of either the tracheid elements or the inner cortical cells.

For most fossil axes the pericycle and phloem are missing leaving the xylem strand separated from the inner cortex which is also separated from the outer cortex, especially where the axis is ribbed (Figs 1-3). The separation of the inner and outer cortex may be due to mechanical causes resulting from the different responses to compression of the two tissues one of whose cells are thick-walled cells and the other parenchymatous. The separation occurs more often immediately below the ribs rather than elsewhere around the perimeter. In contrast the separation of the inner cortex from the xylem probably results from the decay of the nutrient rich phloem and pericycle following the death of the axis. Reconstruction of a stem in cross section (Fig. 6) incorporating the anatomical features discussed above allows for the separation of the tissues in fossil specimens.

That the plant was rhizomic has not been observed directly but has been inferred from a section of an axis which is larger than the

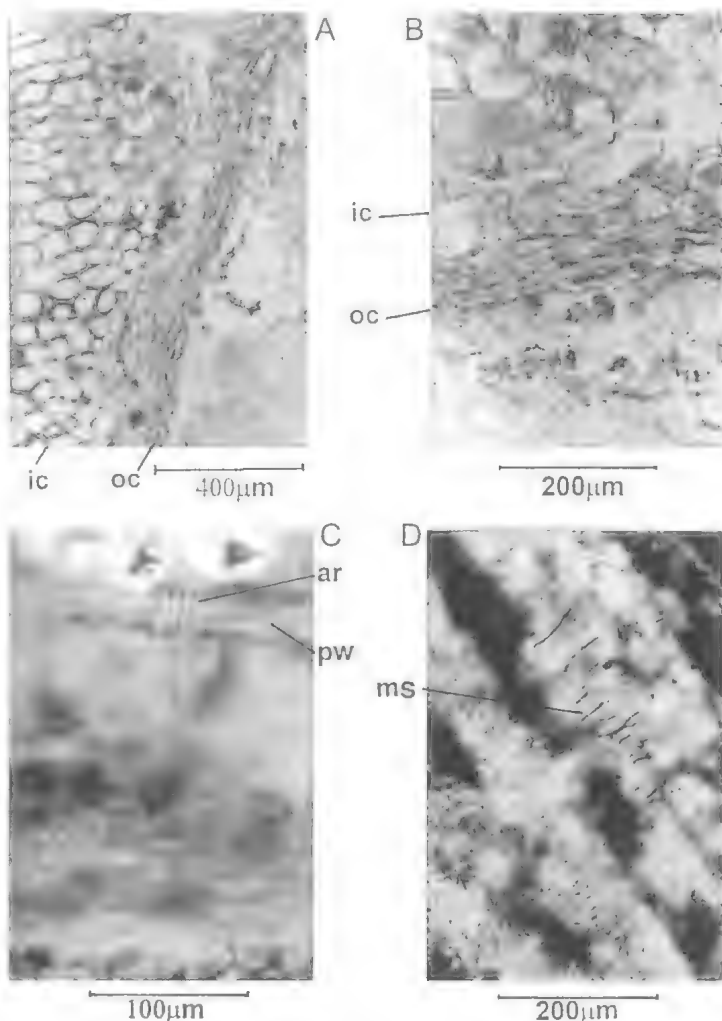


FIG. 4. Anatomical details of *Fanningopteris wyattii* gen. et sp. nov. A, B, transverse sections of cortex. C, longitudinal section of portion of tracheid element with annuli preserved. D, longitudinal section of portion of tracheid element with magnetite strand deposited on primary wall. a, annular ring; ic, inner cortex; oc, outer cortex; ms, magnetite strand; pw, primary wall.

remainder, is elliptical in outline, and whose cortex is not conspicuously differentiated into two contrasting zones (Fig. 1A). Examination of the xylem and cortex tissues reveals that the presumed rhizome has been cut obliquely. Therefore, it may be assumed the axis is circular in section and disposed more or less at right angles to the stems in the section.

As with its proposed rhizomatous habit the dichotomous branching of *Fanningopteris* has been inferred from a section in which most of the

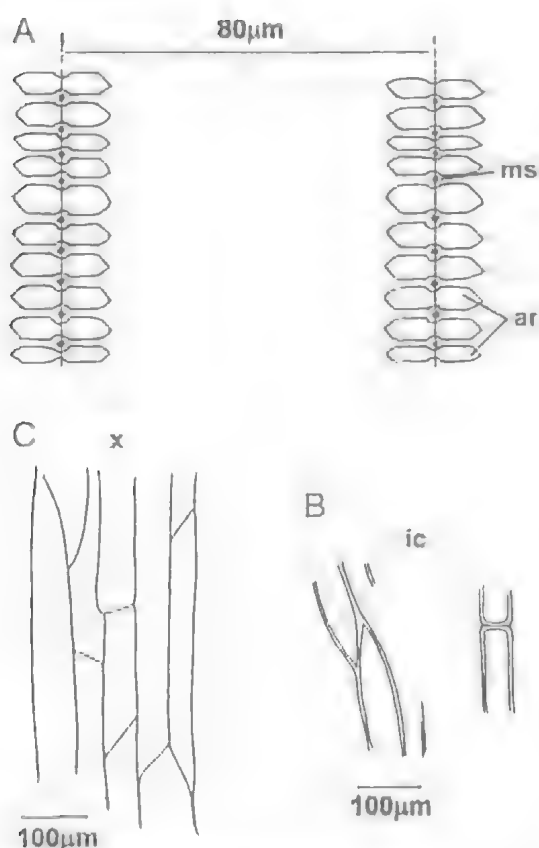


FIG. 5. Tracheid elements and cortical cells of *Fanningopteris wyattii* gen. et spec. nov. in longitudinal section. A, diagrammatic representation of site of deposition of magnetite on primary wall of tracheid element. B, disposition of end walls of inner cortical cells. C, disposition of end walls of tracheid elements. a, annuli; ms, magnetite strand.

stems have been cut transversely. The presence in the section of an axis with two steles suggests it has been cut between the position of the stele dichotomising and the separation of the daughter axes. Whenever two steles (Fig. 2) are present in an axis they differ in size and so are likely to be associated with daughter axes of different diameters a situation that may be observed with the frond segments of extant species of *Lygodium* another protostelic genus.

The habit of *Fanningopteris* is uncertain due to the limited material available. From the appearance of the vascular strands in transverse and vertical section it is apparent the axes, although flexuous and intertwining, are more or less erect and closely packed. They are thereby mutually supportive, but in addition gain

mechanical support from the thick-walled cells of the outer cortex and the ribbing of the axes. Further support may have been afforded by the interlacing of the adventitious roots and rhizomes. This information is, however, inadequate for reconstructing the habit of *F. wyattii*, because it is impossible to know which part of the plant, in terms of height, it represents. If it is the basal parts of the plant that have been preserved, and the rhizomes indicate this may be so, *F. wyattii* would have resembled the Lower Devonian *Zosterophyllum myretonium* (Gensel & Andrews, 1984) or some modern *Schizaea* species.

Otherwise, *Fanningopteris* would have resembled the Lower Carboniferous *Austroclepsis australis* or one of the Cretaceous species of *Tempskya*. These plants were characterised by false stems which formed as a result of the linking together of the basal portions of several intertwining axes in a felt of adventitious leaving the distal portions free as with the modern tree-fern *Todea barbara*.

To distinguish between relative probabilities of these two reconstructions, recourse was had to a comparison of the maximum stem diameter of *F. wyattii* with those of several species some of which had and others did not have false-stems. The maximum diameters of the axes of the several taxa considered are listed in Table 1.

From the Table it is clear that whereas the maximum diameters of species with free standing axes vary from 1.1–4.0 mm those species whose axes become associated into false-stems vary in maximum diameter from 3.5–18.0 mm. Therefore, *F. wyattii* with a maximum axis diameter of 4.7 mm, qualifies, albeit with some uncertainty, for membership of the false-stem group. Further support for believing the species developed false-stems is afforded by its appearance in transverse section, for other than in the sizes of their axes *F. wyattii* and *Austroclepsis australis* are morphologically similar, though differing in anatomy.

DISCUSSION

In the absence of reproductive structures the affinities of *F. wyattii* must be determined solely on the basis of vegetative anatomy. Here all the erect axes have been accepted as stems because they are anatomically similar rather than being of two kinds as would be expected if some were cauline and others petiolar in origin. Having dichotomously branched, leafless stems with

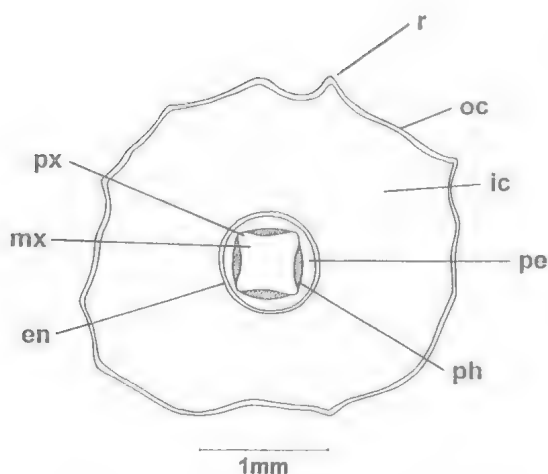


FIG. 6. Reconstruction of a representative axis of *Fanningopteris wyattii* gen. et sp. nov. in transverse section. en, endodermis; ic, inner cortex; mx, metaxylem; oc, outer cortex; pe, pericycle; ph, phloem; px, protoxylem, r, rib.

exarch protoxylem the species has much in common with members of the Zosterophyllophyta but is excluded from that group because of its adventitious roots.

The relations of *F. wyattii* have therefore been sought amongst the ferns as defined by Taylor & Taylor (1993) who list five Orders as having been recorded from Devonian sediments.

The vasculature of all taxa assigned to these Orders is a protostele. Species of Cladoxylales and Iridopteridales have primary xylem strands that are deeply lobed in transverse section whereas those of the Rhacophytales are bar-shaped with peripheral loops at the ends and those of the Zygopteridales are elliptical. Therefore *F. wyattii* is not a candidate for membership of any one of these four Orders. However, notwithstanding its apparent lack of apophyses, because its axes are not separable anatomically into stems and petioles and the xylem strands are quadrangular or triangular in transverse section, the species may be accommodated in Stauropteridales.

Within the Order *F. wyattii* has more in common with *Rowleya trifurcata* than any species of the other two genera. Attention has been drawn above to the similarity of the tracheid elements of *Fanningopteris* to those of *Gosslingia* (Zosterophyllophyta) and in his description of *Rowleya* (Long, 1976) noted that although there is a case for placing the genus in

TABLE 1. The maximum stem diameters of *Fanningopteris wyattii* gen. et sp. nov. and those of some fossil and living taxa with free-standing axes and false-stems. (1) Sahni (1929), (2) Ash & Read (1976), (3) Erwin & Rothwell (1989), (4) Long (1976), (5) Kenrick & Edwards (1988), Taylor & Taylor (1993).

Taxon	Maximum axis diameter (mm)
<i>Fanningopteris queenslandica</i>	4.7
Axes Freestanding	
<i>Gosslingia breconensis</i> (5)	3.0
<i>Sawdonia ovata</i> (6)	4.0
<i>Psilotum nudum</i>	3.7
<i>Stauropteris biseriata</i> (3)	3.2
<i>S. oldhamia</i> (3)	3.4
<i>S. burntislandica</i> (3)	2.0
<i>S. berwickensis</i> (3)	2.5
<i>Gillespiea randolphensis</i> (3)	1.1
Axes aggregated into false-stems	
<i>Austroclepsis australis</i> (1)	18.0
<i>Tempskya wessellii</i> (2)	5.0
<i>T. rossica</i> (2)	7.0
<i>T. superba</i> (2)	15.0
<i>T. grandis</i> (2)	6.0
<i>T. wyomingensis</i> (2)	8.0
<i>T. zolleri</i> (2)	8.0
<i>T. minor</i> (2)	3.5
<i>T. knowltoni</i> (2)	3.5

the Stauropteridales, because of its branching habit and lack of roots it could belong to a more primitive group allied to Psilotaceae.

It is accepted that *F. wyattii* is best included in the Stauropteridales until the structure and arrangement of its sporangia are known. On the basis of this assumption the Cultivation Gully specimen is only the second record of the Order from the Devonian, all others being from the Carboniferous.

The other Devonian record is that of *Gillespiea randolphensis* from the Hampshire Formation near Elkins in West Virginia. This Formation is Famennian (Oliver et al., 1967) and so is about 15 My younger than the Givetian sediments at Cultivation Gully.

Whether *F. wyattii* would be included in the Stauropteridales were its spores and sporangia known is a matter of conjecture.

Likewise, whether the Order represents a single phylogenetic lineage or an artificial assemblage of simple plants with similar

morphologies and anatomical features' (Erwin & Rothwell, 1989) is uncertain. Nonetheless in reporting on a cladistic analysis of vascular plants Rothwell (1996) noted that, with the exception of *Aglaophyton*, the Stauropteridales are the sister group to all other vascular plants. Therefore, the discovery of well-preserved vegetative specimens of *F. wyattii* at a readily accessible locality is important for further searching may reveal the presence of fertile material. Such an exciting discovery would contribute data critical for determining the phylogenetic affinities of all Devonian ferns.

ACKNOWLEDGEMENTS

I thank Alex Cook for drawing my attention to his find and information on stratigraphy and age; Natalie Camilleri for turning my sketches into drawings and preparing plates; Mary Dettmann for photography; Fran Hueber offered a valuable critique of an early draft; Noreen Morris who in response to an enquiry presented me with a transverse section of the type which she cut some years ago.

LITERATURE CITED

- ASH, S.R. & READ, C.B. 1976. North American species of *Tempskya* and their stratigraphic significance. Geological Survey Professional Paper 874: .
- BIERHORST, D.W. 1960. Observations on tracheary elements. *Phytomorphology* 10: 249-305.
- COOK, A.G., LANGE, S.G., DRAPER, J.J. & ZHEN, Y.Y. 1994. Fanning River Group. In Draper, J.J. & Lange, S.G (eds), *Geology of the Devonian to Carboniferous Burdekin Basin*. Queensland Geological Record 1994/9.
- ERWIN, D.M. & ROTHWELL, G.W. 1989. *Gillespiea randolphensis* gen. et sp. nov. (Stauropteridales), from the upper Devonian of West Virginia. *Canadian Journal of Botany* 67: 3063-3077.
- GENSEL, P.G. & ANDREWS, H.N. 1984. *Plant life in the Devonian*. (Praeger Press: New York).
- HARLAND, W.B., ARMSTRONG, R.L., COX, A.V., CRAIG, L.E., SMITH, A.G. & SMITH, D.G. 1990. *A geologic time scale*. (Cambridge University Press: Cambridge).
- HENDERSON, R.A. & CROSDALE, P.J. 1998. Trip 10: Devonian and Carboniferous stratigraphy of the Fanning River-Dotswood area, Burdekin Basin. Pp. 62-71. In Johnson, D.P. (ed.) *Short geological field trips in the Townsville-Charters Towers region*. (14th Australian Geological Convention. Geological Society of Australia: Townsville).
- KENRICK, P. & CRANE, P.R. 1997. The origin and early evolution of plants on land. *Nature*, London 339: 33-39.
- KENRICK, P. & EDWARDS, D. 1988. The anatomy of the Lower Devonian *Gosslingia breconensis* Heard based on pyritized axes, with some comments on the permineralization process. *Botanical Journal of the Linnean Society* 97: 95-123.
- LONG, A. 1976. *Rowleya trifurcata* gen. et sp. nov., a simple petrified plant from the Lower Coal Measures (Westphalian A) of Lancashire. *Transactions of the Royal Society of Edinburgh* 69: 467-481.
- OLIVER, W.A., de WITT, W., DENNISON, J.M., HOSKINS, D.M. & HUDDLE, J.W. 1967. Devonian of the Appalachian Basin. In D.H. Oswald (ed.) *International Symposium on the Devonian System*, Calgary, 1967. Vol.1. (Alberta Society of Petroleum Geologists: Calgary).
- OSBORN, E.M. 1916. Preliminary observations on an Australian *Zygopteris*. Report of the Eighty-fifth Meeting of the British Association for the Advancement of Science (Manchester) 1916: 727-728.
- ROTHWELL, G.W. 1996. Phylogenetic relationships of ferns: a palaeobotanical perspective. In Camus, J.M., Gibby, M. & Johns, R.J., (eds), *Pteridology in perspective*. (Royal Botanic Gardens: Kew).
- SAHNI, B. 1928. On the genera *Clepsydropsis* and *Claoxylon* of Unger, and on a new genus *Austroclepsis*. *New Phytologist* 31:270-278.
1929. On *Clepsydropsis australis*, a zygopterid tree-fern with a *Tempskya*-like false stem from the Carboniferous rocks of Australia. *Philosophical Transactions of the Royal Society of London* 217B:1-37.
- TALENT, J. & MAWSON, R. 1994. Conodonts in relation to age and environmental framework of the Burdekin Basin (Mid-Devonian north-eastern Australia). *Courier Forschungsinstitut Senckenberg* 168: 61-81.
- TAYLOR, T.N. & TAYLOR, E.L. 1993. *The biology and evolution of fossil plants*. (Prentice Hall: Edgeware Cliffs).

A WINGED FRUIT FROM THE TERTIARY OF QUEENSLAND

H.T. CLIFFORD AND MARY E. DETTMANN

Clifford, H.T. & Dettmann, M.E. 2002 5 31: A winged fruit from the Tertiary of Queensland. *Memoirs of the Queensland Museum* 48(1): 79-83. Brisbane ISSN 0079-8835.

A 5-winged fruit from Miocene sediments near Kingaroy, southeast Queensland possesses characters consistent with those of fossil and living apetalous members of *Ceratopetalum* Sm. A flower-like specimen from a similar stratigraphic horizon at a nearby locality is also reminiscent of *Ceratopetalum*, but characters diagnostic of the genus are not preserved. □ *Winged fruit, fossil, Tertiary, Queensland, Australia.*

H. Trevor Clifford, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; Mary E. Dettmann, Department of Botany, The University of Queensland, St Lucia 4072, Australia; 1 February 2002.

A radially symmetrical fossil plant structure comprising five spatulate wings arranged at right angles to the vertical axis and resembling fruits of *Ceratopetalum* Sm. (Cunoniaceae) recently has been recovered from Tertiary sediments near Kingaroy, southeast Queensland. Part and counterpart of the fruit are exposed following splitting of the sediment irregularly along the lateral plane between the upper and lower surfaces of the fruit. Imperfect outlines of the wings and indications of their venation and attachment to a central ovary are displayed. None of the organic matter has survived, but some has been replaced by limonite.

Ceratopetalum fruits in the Australian fossil record were first recognised by Holmes & Holmes (1992) who allocated their species, *C. priscum*, to *Ceratopetalum* after detailed comparisons with fruits of extant species. They demonstrated that sepal venation pattern was a useful discriminatory criterion and concluded that a 5-winged specimen allocated by Ettingshausen (1883) to *Getonites wilkinsonii* Ettings. is also a fossil representative of *Ceratopetalum* rather than having affinities with the Combretaceae as originally suggested. The relationship of the fossil fruits with *Ceratopetalum* was reaffirmed by Barnes & Hill (1999) who described two further species, *C. westermanii* and *C. maslinensis*, from the Tertiary of southeastern Australia.

No other fruits having 4-6 wings are known from Australian Cainozoic sediments in contrast to their frequent representation in Tertiary sediments of Europe, North America, and Asia. Although all the Northern Hemisphere forms are superficially similar in gross morphology, investigation of their ovaries and wing characters has revealed they are taxonomically diverse.

Among the fossil taxa reported (Manchester & Crane, 1987; Manchester, 1991; Manchester & Hably, 1997; Hably & Manchester, 2000; Wang & Manchester, 2000) are *Asterocarpinus*

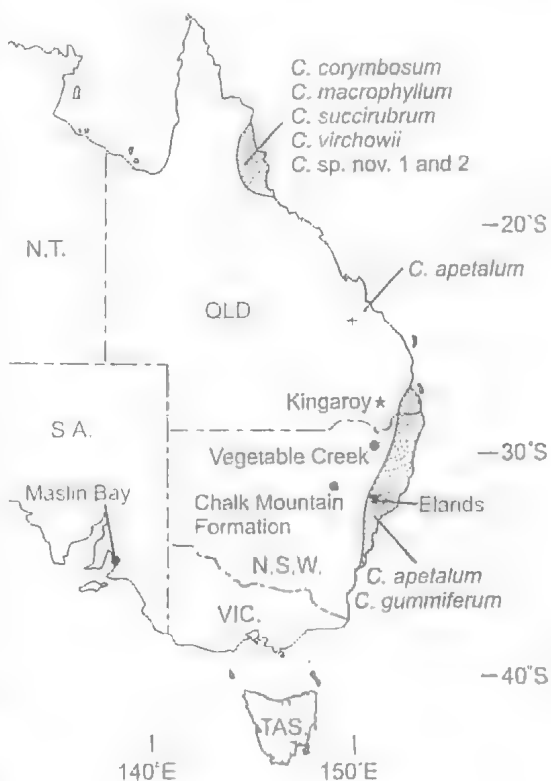


FIG. 1. Map of eastern Australia showing distribution of extant species of *Ceratopetalum* and localities from which fossil fruits of *Ceratopetalum* have been reported (after Barnes & Hill, 1999). + distribution record fide A. Rozefelds; * Kingaroy fossil locality.

Manchester & Crane (Betulaceae), *Chaneya* Wang & Manchester (Simaroubaceae), *Cruciptera* Manchester (Juglandaceae), *Raskya* Manchester & Hably (family affinities possibly with Simaroubaceae), and an extinct member of *Tetrapterys* Cav. emend. A. Juss. (Malphigiaceae).

Notwithstanding imperfect preservation of the fruit fossil from Kingaroy, sufficient characters are represented for comparisons with fruits of *Ceratopetalum* and those of extant and fossil members of several other families.

LOCATION AND AGE

The specimen was collected along with other plant fossils from a ~30cm thick outcrop of ironstained mudstones overlying a thin band of coarse sandstones beneath some 50cm of volcanogenic breccia south of Kingaroy (QML1329 at 26°35'18.6"S 151°56'32.1"E; Fig. 1). Cainozoic sediments in the Kingaroy district formed in small lacustrine basins within an extensive palaeodrainage system, and are considered part of the Tertiary Main Range Volcanics (Sawers & Cooper, 1986), which have been dated as 22-24 my.

SYSTEMATIC PALAEOBOTANY

Family CUNONIACEAE
***Ceratopetalum* Sm., 1793**

TYPE SPECIES. *Ceratopetalum gummiferum* Sm.

***Ceratopetalum* sp.**
(Figs 2, 3A-F, 4A-D)

DIAGNOSIS. Fruit radially symmetrical with five wings disposed in a plane at right angles to a semi-inferior ovary; the wings arise from the margin of a short tube and have longitudinally aligned primary vascular bundles that branch distally to form an imperfect reticulum.

DESCRIPTION. Limonite stained impression of a 5-winged fruit that has split between the upper and lower surfaces of the perianth members that arise from the circular margin of a receptacle ~2 mm in diameter. Calyx members fused at base, lobes spatulate in outline, ~7 mm long, ~4 mm wide and each with 7-9 longitudinal vascular bundles, the central of which enter the receptacle whereas the laterals unite with corresponding bundles in the adjacent lobes below their common sinus. Vascular bundles dichotomise in distal regions of sepals and some of the secondary veins fuse to form an imperfect reticulum.

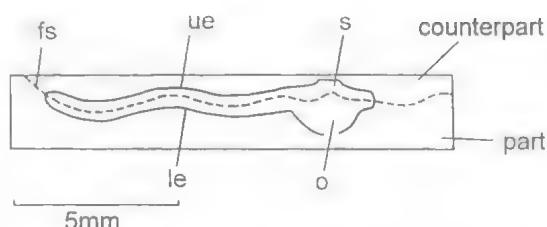


FIG. 2. Transverse section of sediment in which the Kingaroy specimen of *Ceratopetalum* (QMF51124) is preserved (diagrammatic). fs, fracture surface; le, lower epidermis; o, ovary; s, style base; ue, upper epidermis.

Petals not observed. Ovary incompletely preserved; fracture surface concave on part and convex on counterpart. Diameter of fruit 17.5mm.

DISCUSSION. Propeller-like fruits superficially resembling those of the impression occur in many species of dicotyledons distributed amongst at least 12 families belonging to the Rosid, Asterid, and Caryophyllid clades (Magallón et al., 1999). The widespread taxonomic distribution of taxa with such fruits is evident in the sample of extant and fossil genera listed in Table 1. Of those genera only *Ceratopetalum* possesses the set of characters exhibited by the fossil described above which is thus assigned to that genus for the following reasons. The ovary though incompletely preserved is interpreted as semi-inferior as the sepaline whorl arises from the receptacle, and not the pedicel (Fig. 3C,E; Fig. 4B); the sepals arise initially as a short tube from the margin of which develop five lobes; the primary vascular bundles of the sepals are of two kinds in that the central members enter the receptacle but the laterals of adjacent lobes unite in the tissue below their common sinus (Fig. 3C,F; Fig. 4B,C) and in distal regions of the sepals the vascular bundles dichotomise, the dichotomies forming an imperfect reticulum (Fig. 4D); the sepals are constricted at their bases (Fig. 3A,B; Fig. 4A,B). This character set also occurs in *Aphanopetalum* Endl. formerly regarded as closely related to *Ceratopetalum* (Bentham, 1864) but now considered belonging to a clade with *Tetracarpaea*, Haloragaceae and Penthoraceae (Savolainen et al., 2000) or to the Saxifragales (Bradford & Barnes, 2001), but not in other extant and fossil taxa studied with superficially similar 4-6 winged fruits (Table 1). The impression has been assigned to *Ceratopetalum* rather than

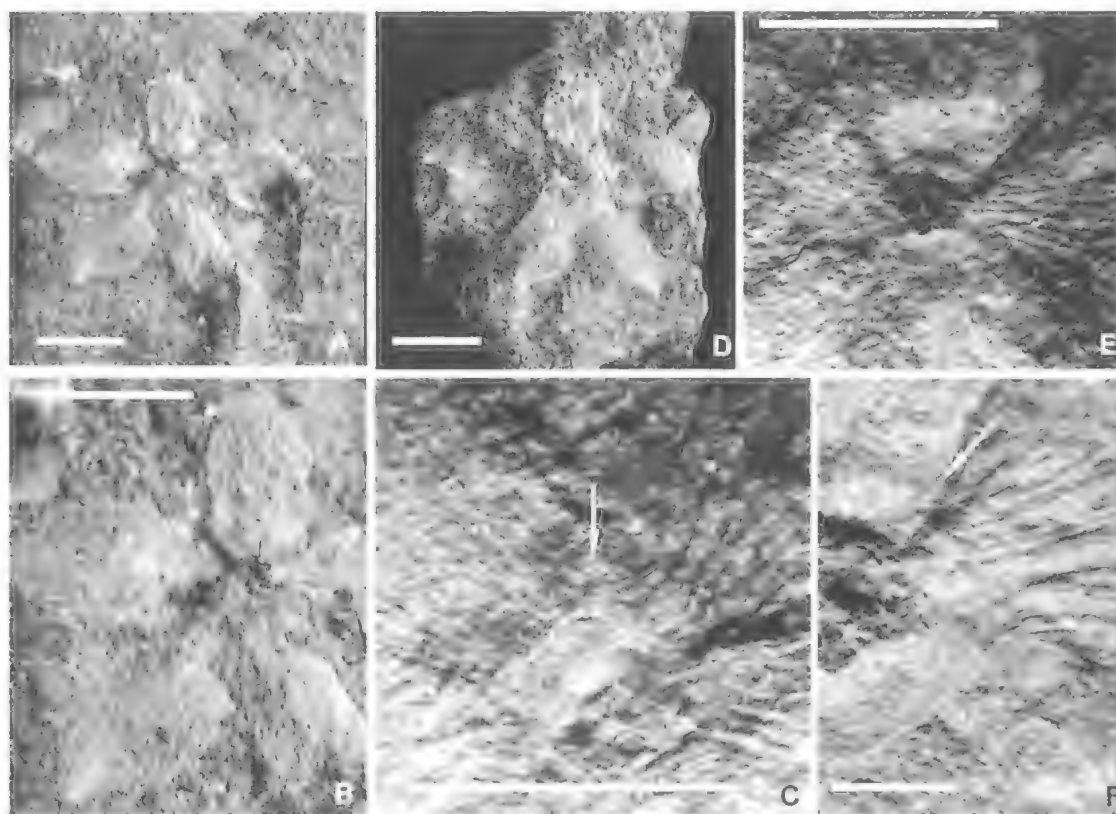


FIG. 3. Fossil fruit of *Ceratopetalum* sp., specimen QMF51124 (A-C) and counterpart (D-F). A, B, showing 5 sepals and impression of ovary, scale bars = 5mm. C, detail of bases of sepal lobes showing vascular traces, and fusion of laterals of adjacent sepal lobes (arrow) near the ovary, scale bar = 2.5mm. D, E, showing venation of sepal lobes and ovary of counterpart, scale bars = 5mm and 2.5mm respectively. F, central area of fruit near ovary showing fusion of lateral vascular strands of adjacent sepal lobes (arrow), scale bar = 1mm.

Aphanopetalum because the latter has four rather than five wings, which are commonly represented in the former genus (Dickson, 1975).

The Kingaroy specimen lacks petals and possesses 7-9 longitudinal primary veins in each sepal lobe and in these respects resembles more closely fruit of extant *Ceratopetalum succirubrum* and *C. virchowii* than fruits of other extant members of the genus. The apetalous fossil taxa, *C. westermanni* Barnes & Hill and *C. maslinensis* Barnes & Hill, differ in possessing sepal lobe venation of three traces. Other described fossil taxa, *C. priscum* Holmes & Holmes and *C. wilkinsonii* (Ettings.) Holmes & Holmes, differ in possessing petals. Although distinct from other fossil taxa we prefer not to institute a formal species pending recovery of further and better preserved specimens.

A limonite compression designated as 'compositaceous compound head' (Hill et al.,

1970, pl. Cz X1, fig. 3; UQF10731) from a nearby locality at Goodyer, some 10km S of Kingaroy has sepal-like structures which in shape and size resemble those of fruits of *Ceratopetalum* (Fig. 5A,B). However, neither the venation pattern nor the structure of the central portion of the fossil has been preserved and so the affinities of the fossil remain in doubt.

Nevertheless, the Kingaroy fruit identified as *Ceratopetalum* sp. confirms the genus in the Queensland Tertiary and extends its known fossil range northwards by some 3° of latitude. Previous reports of fossil fruits of the genus are from Tertiary sediments in South Australia (Christophel & Blackburn, 1978; Christophel, 1994; Barnes, 1999; Barnes & Hill, 1999) and New South Wales (Ettingshausen, 1883; White, 1990; Holmes & Holmes, 1992).

Table 1. Wing and ovary characters of genera with fruits superficially resembling those of *Ceratopetalum*. (e) = extant; (f) = fossil.

Genus	Family	Ovary	No., derivation of wings	Calyx lobes free/united at base	Venation		
					Lateral veins of adjacent lobes united	Number of primary veins/lobe	Vein branching
<i>Ceratopetalum</i> Sm. (e. & f.)	Cunoniaceae	Semi-inferior	4-6, sepals	United	Yes	3-9	Reticulate
<i>Cruciptera</i> Manchester (f.)	Juglandaceae	Inferior	4(5,6), sepals	Free	No	15+	Dichotomous
<i>Asterocarpinus</i> Manchester & Crane (f.)	Betulaceae	Inferior	4-5(6-7), bracts	Free	?	1	Pinnate
<i>Calycopteris</i> Lam. (e.)	Combretaceae	Inferior	5, sepals	United	?	3	Reticulate
<i>Tetrapteryx</i> Cav. (e. & f.)	Malpigiaceae	Superior	4, bracts	United	No	15+	Dichotomous
<i>Petrea</i> L. (e.)	Verbenaceae	Superior	4-6, sepals	United	No	1	Reticulate
<i>Ancistrocladus</i> Wall. (e.)	Ancistrocladaceae	Inferior	5, sepals	United	No	Several	Reticulate
<i>Raskya</i> Manchester & Halby (f.)	?	Superior	4, sepals	Free	No	12-15	Dichotomous
<i>Picrasma</i> Bl. (e.)	Simaroubaceae	Superior	4-5, sepals	United	No	?	Dichotomous
<i>Chaneya</i> Wang & Manchester (f.)	?Simaroubaceae	Superior	5, sepals	United	No	5	Reticulate/Dichotomous
<i>Porana</i> Burm. (e.)	Convolvulaceae	Superior	5, sepals	Free	No	5	Reticulate
<i>Dinetus</i> Sweet (e.)	Convolvulaceae	Superior	4-5, sepals	Free	No	3	Reticulate
<i>Astronium</i> Jacq. (e.)	Anacardiaceae	Superior	6, sepals	?	?	1-3	Dichotomous
<i>Monotes</i> A. DC. (e.)	Dipterocarpaceae	Superior	5, sepals	United	No	5	Reticulate
<i>Waterhousea</i> B. Hyland (e.)	Myrtaceae	Inferior	4-6, sepals	United	No	3	Reticulate

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LITERATURE CITED

- BARNES, R.W. 1999. Palaeobiography, extinction and evolutionary trends in Cunoniaceae (*Ceratopetalum*, *Eucryphia*). Unpubl. PhD thesis, University of Tasmania, Hobart.
- BARNES, R.W. & HILL, R.S. 1999. *Ceratopetalum* fruits from Australian Cainozoic sediments and their significance for petal evolution in the genus. *Australian Systematic Botany* 12: 635-645.
- BENTHAM, G. 1864. *Flora Australiensis: a description of the plants of the Australian Territory*. Vol. 2. (Lovel Reeve & Co.: London).
- BRADFORD, J.G. & BARNES, R.W. 2001. Phylogenetics and classification of Cunoniaceae

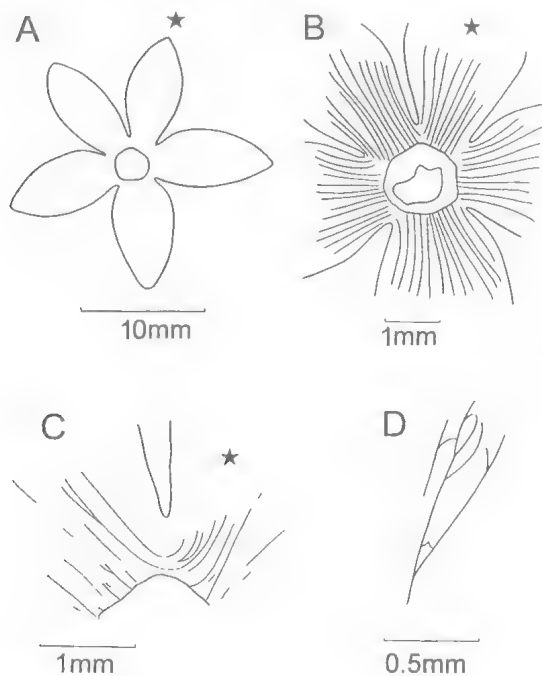


FIG. 4. Fossil fruit of *Ceratopetalum* sp., QMF51124. A, outline of fruit. B, detail of preserved ovary and vascular traces at bases of sepal lobes. C, detail of vascular traces below sinus of two adjacent sepal lobes. D, detail of venation in distal region of sepal lobe.

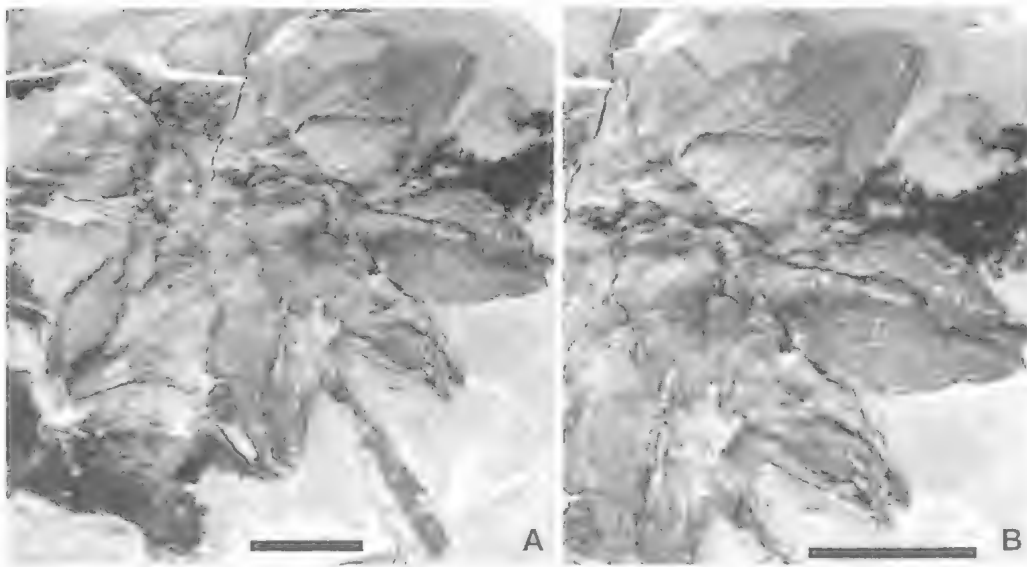


FIG. 5. A,B, fossil specimen (UQF10731) having superficial resemblance to fruits of *Ceratopetalum*, but lacking detail of ovary and wing venation. Scale bars = 5mm.

- (Oxalidales) using chloroplast DNA and morphology. *Systematic Botany* 26: 354-385.
- CHRISTOPHEL, D.C. 1994. The Early Tertiary macrofloras of continental Australia. In Hill, R.S. (ed.) *History of the Australian vegetation: Cretaceous to Recent*: 262-275. (Cambridge University Press: Cambridge).
- CHRISTOPHEL, D.C. & BLACKBURN, D.T. 1978. Tertiary megafossil flora from Maslin Bay, South Australia; a preliminary report. *Alcheringa* 2: 11-27.
- DICKISON, W.C. 1975. Studies on the floral anatomy of the Cunoniaceae. *American Journal of Botany* 62: 433-447.
- ETTINGSHAUSEN, C. von. 1883. Beiträge zur Kenntniss der Tertiärflora Australiens. *Denkschriften Kaiserlichen Akademie Wissenschaften Wien Band I*, 47: 101-148.
- HABLY, L. & MANCHESTER, S.R. 2000. Fruits of *Tetrapterys* (Malphiaceae) from the Oligocene of Hungary and Slovenia. *Review of Palaeobotany and Palynology* 111: 93-102.
- HILL, D., PLAYFORD, G. & WOODS, J.T. (eds) 1970. *Cainozoic fossils of Queensland*. (Queensland Palaeontographical Society: Brisbane).
- HOLMES, W.B.K. & HOLMES, F.M. 1992. Fossil flowers of *Ceratopetalum* Sm. (Family Cunoniaceae) from the Tertiary of eastern Australia. *Proceedings of the Linnean Society of New South Wales* 113: 265-270.
- MAGALLON, S., CRANE, P.R. & HERENDEEN, P.S. 1999. Phylogenetic pattern, diversity, and diversification of eudicots. *Annals of the Missouri Botanical Garden* 86: 297-372.
- MANCHESTER, S.R. 1991. *Cruciptera*, a new juglandaceous winged fruit from the Eocene and Oligocene of western North America. *Systematic Botany* 16: 715-725.
- MANCHESTER, S.R. & CRANE, P.R. 1987. A new genus of Betulaceae from the Oligocene of western North America. *Botanical Gazette* 148: 263-273.
- MANCHESTER, S.R. & HABLY, L. 1997. Revision of "*Abelia*" fruits from the Paleogene of Hungary, Czech Republic and England. *Review of Palaeobotany and Palynology* 96: 231-240.
- SAWERS, J. & COOPER, W. 1986. Kaolin deposits in the Kingaroy area. Pp. 72-76. In Wilmot, W.F. (ed.) 1986 *Field Conference, the South Burnett District*. (Geological Society of Australia, Queensland Division: Brisbane).
- SAVOLAINEN, V., FAY, M.F., ALBACH, D.C., BACKLUND, A., DER BANK, van D., CAMERON, K.M., JOHNSON, S.A., LLEDO, M.J., PINTAUD, J.C., POWELL, M., SHEAHAN, M.C., SOLTIS, D.E., SOLTIS, P.S., WESTON, P., WHITTEN, W.M., WURDACK, M.W. & CHASE, M.W. 2000. Phylogeny of the Eudicots: a nearly complete familial analysis based on *rbcL* gene sequences. *Kew Bulletin* 55: 257-309.
- WANG, Y. & MANCHESTER, R. 2000. *Chaneya*, a new genus of winged fruit from the Tertiary of North America and eastern Asia. *International Journal of Plant Science* 16: 167-178.
- WHITE, M.E. 1990. *The nature of hidden worlds*. (Reed: Sydney).

AN NEW SPECIES OF *Ctenotus* (SCINCIDAE) FROM CENTRAL QUEENSLAND

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Couper, P.J., Amey, A.P. & Kutt, A.S. 2002 531: A new species of *Ctenotus* (Scincidae) from central Queensland. *Memoirs of the Queensland Museum* 48(1): 85-91 Brisbane, ISSN 0079-8835.

Ctenotus rosarium sp. nov., from the Desert Uplands Bioregion of central Queensland is readily distinguished from its congeners by a combination of head scalation (presubocular single, contacting only the subocular supralabial), subdigital lamellae (narrowly callose) and colour pattern (dorsum immaculate between a pale-edged, black vertebral stripe and narrow, black, laterodorsal stripe). The new species occurs in spinifex-dominated open woodland and prefers high hummock grass cover on sandy soils. □ *Ctenotus rosarium* sp. nov., Scincidae, Desert Uplands, Queensland, Australia.

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The Desert Uplands Bioregion of Queensland lies within Australia's northern tropical savannas, straddling the Great Dividing Range between Charters Towers, Hughenden and Blackall (Fig. 1). It borders the Einasleigh Uplands, the Mitchell Grass Downs and the Northern Brigalow Belt (Stanton & Morgan, 1977). This bioregion has been little surveyed, contrasting sharply with coastal eastern Queensland. Australian arid/semi-arid communities are recognised as reptile 'hotspots' (Wilson & Knowles, 1988). Discovery of a new *Ctenotus*, described herein, suggests that the Desert Uplands, with its rich mosaic of acacia and eucalypt woodlands, ephemeral lakes, dune systems and grasslands, is deserving of more attention. The integrity of these habitats is threatened by multiple land-use pressures.

The new *Ctenotus* was first collected from White Mountains National Park in 1994 but the very small sample of one adult and two subadults, one of which was poorly preserved, prevented accurate determination. A further 10 well-preserved specimens now in the Queensland Museum collection enables a formal description.

Because of the large species complement, their frequent sympatry and morphological similarity, *Ctenotus* species have attracted numerous studies on habitat partitioning and ecological interactions (James, 1991; Pianka, 1986; Pianka, 1996; Read, 1998; Sadler, 1987; Twigg et al., 1996). Yet, for many species, habitat preferences are poorly known and the original description remains the only published information. The

voucher specimens were collected as part of a survey incorporating detailed habitat assessment, hence we are also able to define habitat parameters for the new species.

MATERIALS AND METHODS

The new *Ctenotus* was found in close proximity to the similarly-patterned *C. strauchii*. In the field, they were readily separated by a consistent difference in laterodorsal pattern (a narrow, sharply defined stripe in the former vs a broad stripe, containing a series of pale blotches).

All body measurements were taken using Mitutoyo electronic callipers. Supraciliaries, supralabials, infralabials and subdigital lamellae on the fourth toe were counted on both sides of specimens examined. These bilateral counts were averaged for each specimen. The total number of enlarged nuchals is given. Only original tails were included in the morphometric analysis (assessed by eye only). Abbreviations for body measurements are as follows: snout-vent length (SVL); axilla to groin (AG); tail length (vent to tip, TL); forelimb (axilla to tip of longest digit, L1); hindlimb (groin to tip of longest digit, L2); head width (widest point, HW); head length (tip of snout to posterior margin of parietals, HL); snout (tip to anterior margin of orbit, S); eye to ear (posterior margin of orbit to dorsal anterior margin of ear, EE). Comparative details of scalation characters and colour patterns of *Ctenotus* spp. were assessed largely from the descriptions and photographs of Cogger (2000), Hutchinson & Donnellan (1999), Horner (1992), Storr et al. (1999) and Wilson & Knowles (1988).

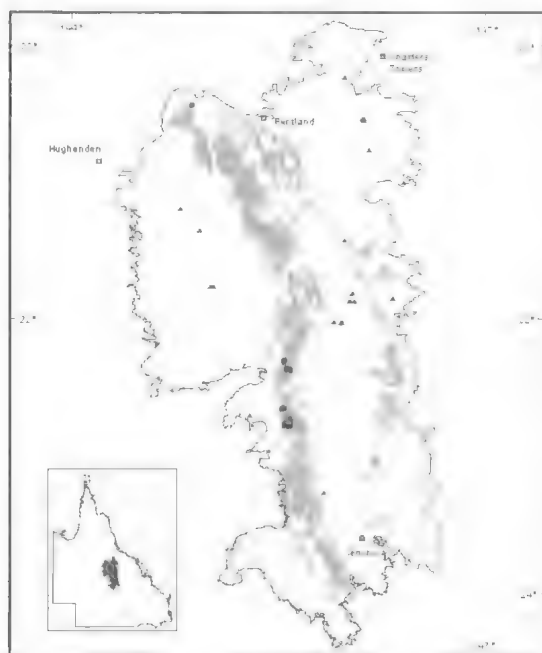


FIG. 1. Map showing trapping localities for *C. rosarium* (bold circle) and *C. strauchii* (bold triangle) in the Desert Uplands bioregion, including the potential distribution for *C. rosarium* according to regional ecosystem association (grey shaded area). Map sources: AUSLIG (1992), Queensland Herbarium (June 2001), Queensland Environmental Protection Agency (1998).

focussing on the *C. schomburgkii* group (Storr, 1981, Shea, Sadler & Swan, unpublished data). Colour pattern terminology follows Wilson & Knowles (1988). Scalation definitions follow Horner (1992).

Broad-scale surveys were conducted within the Desert Uplands (ASK, 1997-2000) to assess vertebrate assemblages of the regional ecosystems (*sensu* Sattler & Williams, 1999). Sampling utilised a standardised nested quadrat array as the basic trapping unit (after Woinarski & Fisher, 1995), using pitfall, Elliott and cage traps over a 96 hour period, and timed active searches.

Detailed habitat variables measured at each site were: location, altitude, season, landform, distance to water, level of fire, weed and cattle disturbance, % cover of ground strata elements (rock, tussock and hummock grass, bare ground, sedges, forbs, ferns), soil characteristics (colour, texture, degree of cracking), log and litter cover, height, cover, diversity and basal area of vegetation strata. Mann-Whitney-U tests were

conducted to identify environmental variables determining presence or absence of the new *Ctenotus*.

SYSTEMATICS

The current diagnosis of *Ctenotus* Storr, 1964 is not based on derived characters. Our assignment rests on the following external characters (Cogger, 2000): limbs pentadactyl, absence of supranasal scales, eyelids moveable and scaly, parietal scales in contact behind the interparietal, conspicuous anterior ear lobules, smooth body scales, and a colour pattern of dorsal and lateral longitudinal stripes and other markings. The type series is deposited in the Queensland Museum.

Ctenotus rosarium sp. nov. (Figs 2-4)

ETYMOLOGY. Latinised English – rosary beads; a noun in apposition. Alluding to the series of pale blotches along the lateral zone which resembles a string of beads.

MATERIAL. HOLOTYPE QMJ72577 Fortuna Stn, 50km N Aramac (22°43'50"S, 145°35'39"E). PARATYPES QMJ58559-61 White Mountains NP, Hughenden (20°26'48"S 144°50'05"E); QMJ68680 Fortuna Stn, 45km N Aramac (22°45'51"S 145°35'35"E); QMJ72578 type locality; QMJ72579-80, Fortuna Stn, 50km N Aramac (22°44'46"S 145°35'47"E); QMJ72751-3 Bede Stn, 110km NNE Aramac (22°22'15"S 145°35'00"E); QMJ73350 Albionvale Hstd, 100km N Aramac (22°18'14"S 145°33'01"E); QMJ73655, White Mountains NP (20°26'32"E 144°52'35"E).

DIAGNOSIS. Maximum adult SVL in type series = 43.8mm (maturity assessed by gonad examination); 26-29 midbody scale rows. Colour pattern most like that of southwestern *C. schomburgkii* (dorsum immaculate between a pale-edged, black vertebral stripe and narrow, black laterodorsal stripe, upper lateral zone black with a single series of pale blotches, Fig. 4). It is distinguished from all similarly-patterned *Ctenotus* spp. by the following characters combined: presubocular single (Fig. 5), usually greatly reduced and contacting only the subocular supralabial (usually 5th); prefrontals moderate, widely separated (Fig. 3); subdigital lamellae narrowly callose.

DESCRIPTION. *Measurements.* SVL (mm) 26.6-43.8 (mean=39.1, standard deviation, S.D.=5.0, n=12). Proportions (%SVL): AG=47.1-52.4 (mean=48.9, S.D.=2.0, n=12); TL=164-210 (mean=192, S.D.=17, n=5); L1=29.5-36.2 (mean=32.4, S.D.=1.89, n=12); L2=47.3-57.0 (mean=52.2, S.D.=3.1, n=12); HL=



FIG. 2. *Ctenotus rosarium* in life, paratype QMJ73350 from Albionvale Hsd, 100km N Aramac (22°18'14"S 145°33'01"E). (photograph by A.S. Kutt)

20.2–25.2 (mean=21.5, S.D.=1.3, $n=12$). Proportions (%HL): HW=55.8–67.6 (mean=63.1, S.D.=3.9, $n=13$); S=42.5–48.3 (mean=45.4, S.D.=1.7, $n=13$); EE=35.8–44.8 (mean=39.8, S.D.=2.7, $n=13$).

Scalation. Nasals in narrow to moderate contact; nasal groove absent; prefrontals moderate, widely separated; maximum length of frontal 1.6–1.9 times maximum width, (mean=1.7, S.D.=0.1, $n=13$); frontal usually contacts frontonasal, prefrontals, first three supraoculars (rarely two, QMJ72751 & QMJ58559 one side only) and frontoparietals, and is narrowly separated from first supraciliary (rarely in contact, QMJ72752, QMJ72580, QMJ72579 both sides; QMJ73655 one side only); supraoculars four, second largest; supraciliaries 6–8 (mean=7.2, S.D.=0.6, $n=13$), first largest; frontoparietals paired and distinct from interparietal; enlarged nuchals 7–11 (mean=8.5, S.D.=1.4, $n=13$); loreals 2, second largest; preoculars 2; presubocular single, usually greatly reduced and contacting only the subocular supralabial (Fig. 5A; see Variation in Paratypes); supralabials 7, 5th subocular, rarely 5, 3rd subocular (QMJ72753 one side only) or 8, 6th subocular (QMJ68680 both sides); infralabials 6, rarely 7 (QMJ58560 one side only), 2–3 in contact with postmental (mean=2.1, S.D.=0.3, $n=13$); ear opening large, vertically elliptic with 3–8 lobules on anterior edge; Midbody scale rows 26–29 (mean=27.7, S.D.=1.0, $n=12$); paravertebral scales, from anterior-most nuchal to posterior margin of hindlimb, 55–64 (mean=58.7, S.D.=2.7, $n=12$); lamellae beneath fourth toe

19–26 (mean = 22.5, S.D. =1.6, $n=13$), narrowly callose, pigmented; a single row of supradigital scales present along almost the entire length of the fourth toe.

Measurements and scale counts for the holotype (QMJ72577) are: SVL=40.5mm; AG=21.2mm; TL=78.5mm; L1=13.6mm; L2=21.8mm; HW=5.7mm; HL=8.7mm; S=4.1mm; EE=3.32mm; maximum length of frontal 3.8mm; maximum width of frontal 2.2mm; supraciliaries 8, first largest; enlarged nuchals 10; supralabials 7, 5th subocular; infralabials 6; ear lobules 7; midbody scale rows 28; paravertebrals 55; lamellae beneath fourth toe 23.

Colour Pattern. Dorsal ground colour bronze. Longitudinal stripes and zones are: vertebral black and narrow with pale edging (Fig. 4, stripe 5), extending from nuchals to base of tail; narrow black laterodorsal (Fig. 4, stripe 4), bordered below by copper dorsolateral (Fig. 4, stripe 3); broad chocolate brown upper lateral zone, commencing at tip of snout and extending full length of tail, containing a single series of copper blotches along flanks (Fig. 4, stripe 2); midlateral white from loreals to tail (Fig. 4, stripe 1); lower

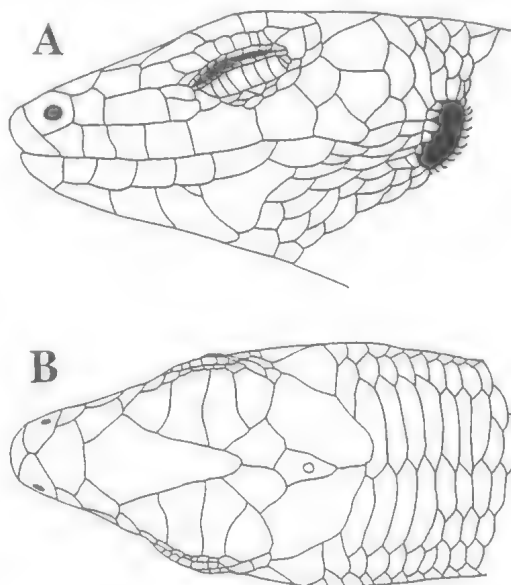


FIG. 3. *Ctenotus rosarium*, holotype, QMJ72577, head in lateral (A) and dorsal (B) views.

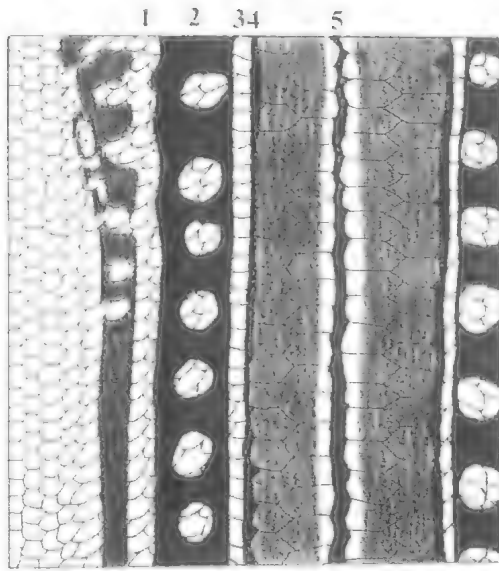


FIG. 4. Schematic diagram (after Storr et al., 1999) showing the colour pattern of *C. rosarium*. 1 = midlateral stripe, 2 = upper lateral, 3 = dorsolateral, 4 = laterodorsal, 5 = vertebral.

lateral dark brown, containing obscure anterior blotches; ventral surface white; limbs bronze with dark brown stripes.

Variation in Paratypes. In QMJ72751 and QMJ72753 the presubocular contacts both the preocular supralabial and the subocular supralabial (QMJ72753 left side only). In QMJ58561 the pale blotches of the upper lateral zone appear as a double series because the pale dorsolateral stripe is fragmented. In QMJ58559, QMJ72753 and QMJ73655 the vertebral stripe is incomplete (confined to nuchal area QMJ58559; disappearing half way between the axilla and groin QMJ72753; present on anterior body and base of tail QMJ73655).

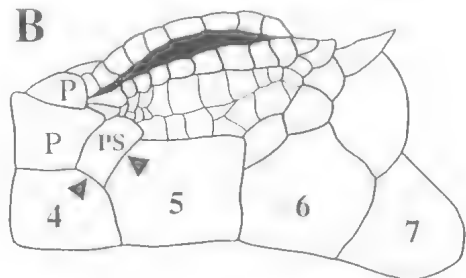
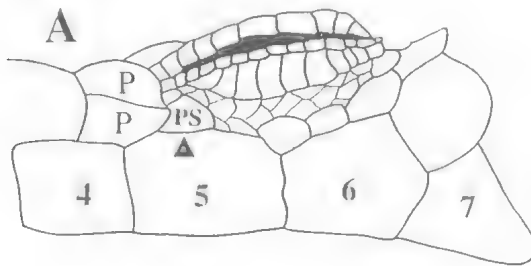


FIG. 5. Comparison of presubocular/supralabial contact between A. *Ctenotus rosarium* holotype QMJ72577, B. *Ctenotus strauchii*, QMJ58660. P = preocular, PS = presubocular, 4-7 = supralabials.

COMPARISON WITH OTHER SPECIES. *Ctenotus rosarium* can be distinguished from other similarly-patterned *Ctenotus* spp. by the combination of characters given in the diagnosis. In colour pattern, it is most like the *C. schomburgkii* group (*allotropis*, *brooksi*, *schomburgkii*, *strauchii*, and *tantillus*). It is distinguished from these, except *C. brooksi*, by the presubocular/supralabial contact (presubocular greatly reduced and contacting subocular supralabial only [Fig. 5A], vs presubocular contacting preocular supralabial and subocular supralabial [Fig. 5B]), apart from aberrant specimens (Table 1). The narrowly callose subdigital lamellae (vs sharply keeled lamellae) further separates *C. rosarium* from all members of the *C. schomburgkii* group, except *C. allotropis*, which differs in dorsal pattern (*C. rosarium* with a narrow, sharply defined laterodorsal stripe vs a broad laterodorsal stripe, containing a series of pale blotches). The only species outside the *C. schomburgkii* group with which *C. rosarium* can be confused are *C. monticola* (to which it would key in Cogger, 2000) and *C. arnhemensis*. It is separated from both by the presubocular/supralabial contact (Fig. 5). It is further separated from *monticola* by upper lateral pattern (single row of spots vs spots forming transverse bars) and *arnhemensis* by the width of the vertebral stripe (very fine vs moderately wide).

DISTRIBUTION. *Ctenotus rosarium* occurs in a narrow band of deep red sandy earths, between 20°S-23°S in the Desert Uplands Bioregion. (Fig. 1), where it is strongly associated with particular vegetation and soil types.

HABITAT. *Ctenotus rosarium* is a terrestrial, diurnal lizard occurring in spinifex-dominated open woodlands. The species was found sheltering beneath dense spinifex hummocks and within burrows located in their bases. Trapping shows greater activity during summer (3.0 per

TABLE 1. Frequency of presubocular/supralabial contact states shown in Fig. 5.

Species	5A both sides	Sides different	5B both sides
<i>Ctenotus rosarium</i>	11	1	1
<i>Ctenotus allotropis</i>	0	0	10
<i>Ctenotus arcanus</i>	0	0	16
<i>Ctenotus arnhemensis</i>	0	0	6
<i>Ctenotus brooksi</i>	38	3	3
<i>Ctenotus hilli</i>	0	0	6
<i>Ctenotus monticola</i>	0	0	3
<i>Ctenotus nullum</i>	0	0	12
<i>Ctenotus schomburgkii</i>	5	1	39
<i>Ctenotus strauchii</i>	2	3	60
<i>Ctenotus tamillus</i>	0	1	5

quadrat in wet season, October–March, 1.5 per quadrat in dry season, April–September). During the warmest months, activity extends to dawn and dusk.

During this study, *C. rosarium* was found only in the extensive, uniform, gently undulating Cainozoic sand deposits along the Great Dividing Range (through the centre of the Desert Uplands). Specimens from Bede, Albionvale and Fortuna Stations were trapped predominantly within the low, open Yellowjack (*Eucalyptus similis*) woodlands with a moderate to dense spinifex (*Triodia pungens*) groundcover (regional ecosystem 10.5.1, Sattler & Williams, 1999; Fig. 6). Specimens were also captured at these localities in small patches of mixed *E. similis*, *Corymbia brachycarpa*, *Corymbia setosa*, *Corymbia dallachiana* woodlands (regional ecosystem 10.5.2, Sattler & Williams, 1999), interspersed and contiguous to the vegetation above. At White Mountains NP, specimens were trapped in open woodlands of *Corymbia leichhardtii*, *C. brachycarpa*, *Eucalyptus quadricostata* and *C. erythrophloia*, with a mixed *Triodia bitextura*/assorted tussock groundcover (regional ecosystem 10.5.9, Sattler & Williams, 1999). This vegetation type is associated, continuous and intergrading with the *E. similis*-dominated communities, and the floristic change reflects latitudinal, altitudinal and climatic gradients. Of the 196 quadrats examined, *C. rosarium* was trapped only in the above communities. A total of 63 individuals were trapped in 23 of 47 quadrats in the *E. similis* mosaics, while one individual was trapped in 5 quadrats sampled at White Mountains NP.

Table 2. Average scores for habitat variables with significant differences (Mann-Whitney-U test) between *C. rosarium* present and absent sites. Only significant variables are listed given the large number of variables examined (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

Habitat variable	Present	Absent	P
Foliage projective cover >10m	0.29	0.69	***
Foliage projective cover 1–3m	1.86	1.34	***
Forb cover (%)	3.05	6.64	***
Hummock grass cover (%)	40.24	11.26	***
Rock cover (%)	0.00	2.84	***
Sedge cover (%)	0.00	2.11	***
Tussock grass (%)	12.4	26.9	***
Rock cover 2–6cm (1=<2% to 6=75–100%)	0.00	0.31	***
Rock cover 0.6–2cm (1=<2% to 6=75–100%)	0.05	0.50	***
Soil type (1=sand to 5=clay)	1.14	2.79	***
Canopy height (m)	8.95	10.08	*
Number of species in ground strata	10.19	13.06	*

Analysis of environmental variables (Table 2) indicates that *C. rosarium* favours sites with less dense tree cover and height, and higher low shrub cover with ground stratum of low diversity including:– high hummock grass, low forb, sedge and tussock grass. The sandy soils are without rock.

Generalised linear modelling (Poisson error distribution) was undertaken to examine the effects of grazing and fire on a range of vertebrates within a small subset of *E. similis* quadrats ($n=36$) in the Desert Uplands bioregional survey (ASK unpublished data). Grazed areas are stocked at consistent rates due to moderate carrying capacities. Historically, due to Heat-leaf Poison Bush *Gastrolobium grandiflorum*, many paddocks in the region are ungrazed.

The minimum adequate model identified grazing as a significant factor (intercept -0.332, grazing 0.654, $p < 0.01$, total deviance explained 55%), with *C. rosarium* being less abundant in grazed sites (0.36/quadrat) than ungrazed sites (1.93/quadrat). Kruskal-Wallis analysis of variance by ranks indicated a significant change in some habitat variables (all $p < 0.001$) due to grazing (bare ground cover increase 39.3–53.2%, hummock grass cover decline 46.3–21.1%, tussock grass cover increase 5.4–13.2%) inferring a



FIG. 6. *Eucalyptus similis* habitat of *C. rosarium*, Fortuna Stn, 50km N Aramac (22°46'34"S 145°35'40"E) photograph by A.S. Kutt.

positive relationship between *C. rosarium* abundance and intermediate to high ground cover of hummock grasses. No significant fire effect was noted.

REPRODUCTION. QMJ72578 (SVL=40.6mm) and QMJ58560 (SVL=43.8mm) were dissected to determine that the larger individuals in the series were mature. Male QMJ72578 was in peak reproductive condition with testes enlarged and the epididymis opaque and turgid. It was collected mid December. A second male, QMJ58560, collected in early March, had a regressed testis and the epididymis, while still opaque, was flaccid. We did not attempt to assess minimum reproductive size.

DIET. The gut of QMJ58560 contained fragments of an ant (Hymenoptera, Formicidae, *Cerapachys* sp.) and one stinkbug nymph (Hemiptera, Pentatomoidea). QMJ72758 contained an adult weevil (Coleoptera, Curculionidae).

COMMENTS. In colour pattern, *C. rosarium* most closely resembles members of the *C. schomburgkii* species group (Storr, 1981; Storr et al., 1999) but it is precluded from this group by

the absence of mucronate keels on its subdigital lamellae. It could equally well be assigned to a number of other species groups, including the *C. lesueurii* or *C. leonhardii* groups. While we are not concerned with the placement of *C. rosarium* within the 'species-group' concept, we recognise these groups as units of convenience. Their validity as monophyletic assemblages is questionable (Pianka, pers. comm. 1996, preliminary phylogeny: <http://uts.cc.utexas.edu/~varanus/ctenotus.html>) and requires further study (Hutchinson & Donnellan, 1999; Aplin & Smith, 2001). The original diagnoses are loose and have not been redefined to accommodate new species. Placement of any species within the existing scheme is largely subjective.

Marked allopatry is seen between *C. rosarium* and *C. strauchii*, the only similarly-sized and patterned species in the Desert Uplands Bioregion, and there is partitioning between the habitat types in which they occur. *C. strauchii* was trapped in 12 regional ecosystems which consisted of low open acacia woodlands (*Acacia argyrodendron*, *A. harpophylla*, *A. cambagei*, *A. shirleyi*), riparian woodlands (*Eucalyptus camaldulensis*, *E. coolabah*), iron bark woodlands (*Eucalyptus whitei*, *E.*

melanophloia), heath, shrubland and sparse rocky woodland types. In some places the transition from one species to the other was sharp, particularly on the sandy soils where *E. whitei/melanophloia* dominated communities on yellow earths rapidly change into *E. similis* dominated communities on deep red sands. All records of *C. rosarium* are within *E. similis* and associated regional ecosystems on the deep red sands of the Alice Tableland. *C. strauchii* has been found in the neighbouring ironbark and other vegetation types, suggesting that regional ecosystem type may be a reasonable predictor for the distribution of both species.

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LITERATURE CITED

- APLIN, K.P. & SMITH, L.A. 2001. Checklist of frogs and reptiles of Western Australia. Records of the Western Australian Museum supplement No. 63:51-74.
- COGGER, H.G. 2000. Reptiles & amphibians of Australia. (Reed New Holland: Sydney).
- HORNER, P. 1992. Skinks of the Northern Territory. Northern Territory Museum of Arts and Sciences Handbook Series No 2.
- HUTCHINSON, M.N. & DONNELLAN, S.C. 1999. Genetic variation and taxonomy of the lizards assigned to *Ctenotus uber orientalis* Storr (Squamata: Scincidae) with description of a new species. Records of the South Australian Museum 32(2): 173-189.
- JAMES, C.D. 1991. Temporal variation in diets and trophic partitioning by coexisting lizards (*Ctenotus*: Scincidae) in central Australia. *Oecologia* 85(4): 553-61.
- PIANKA, E.R. 1986. Ecology and natural history of desert lizards: analyses of the ecological niche and community structure. (Princeton University Press: New Jersey).
1996. Long-term changes in lizard assemblages in the Great Victoria Desert. Dynamic habitat mosaics in response to wildfires. Pp191-215. In Cody, M.L. & Smallwood, J.A. (eds) Long-term studies of vertebrate communities. (Academic Press: San Diego).
- READ, J.L. 1998. The ecology of sympatric scincid lizards (*Ctenotus*) in arid South Australia. *Australian Journal of Zoology* 46(6): 617-629.
- SADLIER, R. 1987. Distribution by habitat of six *Ctenotus* species in SW N.S.W. *Herpetofauna* 17(1):1-4.
- SATTLER, P. & WILLIAMS, R. 1999. (eds) The conservation of Queensland's regional ecosystems. (Environmental Protection Agency: Brisbane).
- STANTON, J.P. & MORGAN, G. 1977. The rapid selection and appraisal of key and endangered sites. The Queensland Case Study. University of New England, School of Natural Resources Report, No. PR4.
- STORR, G.M. 1981. Ten new *Ctenotus* (Lacertilia: Scincidae) from Australia. Records of the Western Australian Museum 9(2): 125-46.
- STORR, G.M., SMITH, L.A. & JOHNSTONE, R.E. 1999. Lizards of Western Australia. I Skinks. (Western Australian Museum: Perth).
- TWIGG, L.E., HOW, R.A., HATHERLY, R.L. & DELL, J. 1996. Comparison of the diet of three sympatric species of *Ctenotus* skinks. *Journal of Herpetology* 30(4): 561-566.
- WILSON, S.K. & KNOWLES, D.G. 1988. Australia's Reptiles. (Collins: Sydney).
- WOINARSKI, J.C.Z. & FISHER, A. 1995. Wildlife of lancewood (*Acacia shirleyi*) thickets and woodlands in northern Australia. 1. Variation in vertebrate species composition across the environmental range occupied by lancewood vegetation in the Northern Territory. *Wildlife Research* 22: 379-412.

A WESTERN RANGE EXTENSION FOR THE SKINK *SAIPHOS EQUALIS*. *Memoirs of the Queensland Museum* 48(1): 92. 2002:- The fossorial skink *Saiphos equalis* occurs on the coast and adjacent ranges of southern NSW northward to extreme SE Queensland (Cogger, 2000). Wilson & Knowles (1992) defined the Queensland range as extending to Kroombit Tops and noted that the species becomes increasingly altitude-dependent in the north of its range. Specimen records from the Queensland Museum indicate that the specimens were collected at locations on the Great Dividing Range, its spurs and associated subcoastal ranges. The majority of records are from the Border Ranges and Granite Belt regions, but they extend as far north as Kroombit Tops and west to the Bunya Mountains. The Dept of Natural Resources Forestry database contains records for Diamondy State Forest, on the Great Dividing Range NW of the Bunya Mountains (M. Mathieson pers. comm.). Sorley (1997) referred to the species in the Chinchilla area, but I have been unable to find the original source of this record - the species may be present in forests on the nearby ranges.

I captured a *Saiphos equalis* on 9 March 2001 during flora and fauna surveys of a proposed nature refuge on 'Oakwells', west of Injune. 'Oakwells' is a cattle grazing property located on the Great Dividing Range, just N of Mt Hutton. The capture site was an area of basalt scree, vegetated with dry vine forest, on the steep upper slopes of Main Top at 25°45'05"S, 148°16'29"E and approximately 840m altitude. The skink was located under loose rock infilled with leaf mulch and humus. The specimen is lodged with the Queensland Museum (QMJ76305).

'Oakwells' is about 270km NW of Chinchilla and about 320km WNW of Diamondy State Forest, thus representing a considerable extension westward of the known range of this skink. The question arises whether this record represents an isolated population or whether the distribution is continuous along the Great Dividing Range. To the north of Injune, the Great Dividing Range meets the extensive uplands of the Carnarvon and Expedition Ranges. These uplands have been described as 'islands' in the mesotherm archipelago of Nix (1993). More temperate conditions here are associated with outlier or relict populations of Bassian herpetofaunal

elements more typical of SE Australia. Examples known to occur in the Carnarvon Ranges are the frog *Adelotis brevis*, the skinks *Calypotis scutirostrum*, *Ctenotus arcanus* and *Egernia cunninghamii* and the elapid snake *Notechis scutatus* (Craig Eddie, QPWS, pers. comm.). *Saiphos equalis* could be another such relict species, but to date has not been located in fauna surveys of the national parks of the area. It would be useful to confirm *Saiphos equalis* in the Chinchilla area. Some fauna surveys have been carried out in Barakula State Forest, which straddles the Great Dividing Range to the north of Chinchilla (M. Mathieson, L. Hogan pers. comm.). To date, the species has not been found there. More surveys, perhaps targeting the more mesic habitats, are needed to define the western limits of the range of this cryptic lizard.

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Literature Cited

- COGGER, H. 2000. Reptiles and Amphibians of Australia. 6th ed. (Reed: Sydney).
- NIX, H.A. 1993. Bird distributions in relation to imperatives for habitat conservation in Queensland. Pp. 12-21. In Catterall, C.P., Driscoll, P.V., Hulsman, K., Muir, D. & Taplin, A. Birds and their Habitats: Status and Conservation in Queensland. (Qld Ornithological Society: Brisbane).
- SORLEY, J. 1997. Reptiles of the area. Pp. 77-82. In Hando, R. & Hando, V. (eds.), Going Bush with Chinchilla Nats. 2nd ed. (Chinchilla Field Naturalists' Club: Chinchilla).
- WILSON, S.K. & KNOWLES, D.G. 1992. Australia's Reptiles. A Photographic Reference to the Terrestrial Reptiles of Australia. (Cornstalk Publishing: Pymble).

Richard Johnson, Queensland Parks and Wildlife Service, PO Box 981, Roma 4455, Australia; 30 August 2001.

IDENTIFICATION AND EVOLUTION OF AUSTRALIAN TORRENT TREEFROGS (ANURA: HYLIDAE: *LITORIA NANNOTIS* GROUP)

MICHAEL CUNNINGHAM

Cunningham, M. 2002 5 31: Identification and evolution of Australian Torrent Treefrogs (Anura: Hylidae: *Litoria nannotis* group). *Memoirs of the Queensland Museum* 48(1): 93-102. Brisbane. ISSN 0079-8835.

All four species of Australian Torrent Treefrogs (*Litoria nannotis* group) have declined since 1990 and are classified as Endangered. I address confusion in identification and reconstruct evolutionary relationships among Torrent Treefrogs. Species differ particularly in size, calls, head shape, webbing, and secondary sexual characteristics such as the form and distribution of nuptial spinules. Torrent Treefrogs are united by spinose nuptial pads, *Litoria rheocola* is basal within the group and the clade (*nyakalensis*, (*lorica*, *nannotis*)) is defined by coarse nuptial spines, enlarged thumbs in males, and robust forearms. The only external characters which separate *nannotis* from *lorica* are size and slight differences in snout shape. Mitochondrial DNA from *nannotis* and *rheocola* suggest that this group arose well before the late Miocene - Pliocene contraction of rainforest in eastern Australia. *Litoria lorica* is known from two published localities on the Thornton uplands. I report two further localities, one of which represents the last sighting of *lorica* in the wild, and a series of museum specimens from Carbine Tableland. Neither *nyakalensis* nor *lorica* have been seen since 1991 and they should be classified as Critically Endangered. Recent discoveries of other declining species and this range extension for *lorica*, suggest a need for intensive surveys of the Carbine and Thornton uplands. □ *Litoria*, decline, phylogeny, distribution, conservation.

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Australian Torrent Treefrogs comprise four species of *Litoria* (Australian Waterfall frog, *nannotis*; Common Mistfrog, *rheocola*, Mountain Mistfrog, *nyakalensis*, and Armoured Mistfrog, *lorica*) which, although modest, is the second-most speciose vertebrate radiation in the Wet Tropics rainforests (after *Cophixalus* frogs, with ten endemic species). Torrent Treefrogs share adaptations to life along torrent streams, such as dorsoventrally flattened, suctorial tadpoles, and adults are rarely observed away from riparian microhabitats (Hodgkison & Hero, 2002). These species differ in appearance, habitat choice and life history. *Litoria nannotis* is usually confined to areas around cascades and waterfalls, with tadpoles generally found under rocks in cascades (Hodgkison & Hero, 2001). *Litoria lorica* closely resembles *nannotis* and appears to be similarly confined to cascades along torrent streams. *Litoria nyakalensis* and *rheocola* resemble each other in appearance and ecology and are more evenly distributed along streams than the preceding two species (Liem, 1974). *Litoria nannotis*, *rheocola* and *nyakalensis* differ markedly in mating calls (Hero & Fickling, 1994) but due to their torrent stream habitat these calls are difficult to record and have not been

compared among populations, within species. The call of *lorica* has not been described.

Distributional records of Torrent Treefrog species are nested across altitudes and latitudes (Fig. 1) but see below for current distribution. All four species occurred in sympatry at several upland sites on the Thornton Massif (145° 20' 26"E, 16° 03' 11"S), and *lorica* is known only from these sites (Covacevich & McDonald, 1993), and from a site on the Carbine Tableland, reported here. *Litoria nyakalensis* occurred with *nannotis* and *rheocola* above 400m, between the Thornton Massif and the Kirrama Range (145° 48'E, 18° 13'S) (McDonald, 1992). Bioclimatic models predict suitable climates for *nyakalensis* on the Windsor Tableland to the northwest, (144° 58'-145° 09'E, 16° 10'-18'S), but it has not been recorded in this area (Nix & Switzer, 1991). *Litoria rheocola* has a wide distribution in lowlands and uplands between Amos Bay (145° 19'-20'E, 15° 41'S) at the northern end of the Wet Tropics rainforest, and Broadwater Ck (145° 57'E, 18° 23'S) near the Herbert River (Covacevich & McDonald, 1993). *Litoria nannotis* occurs throughout the distribution of the other three species, from foothills to uplands, and is the sole species

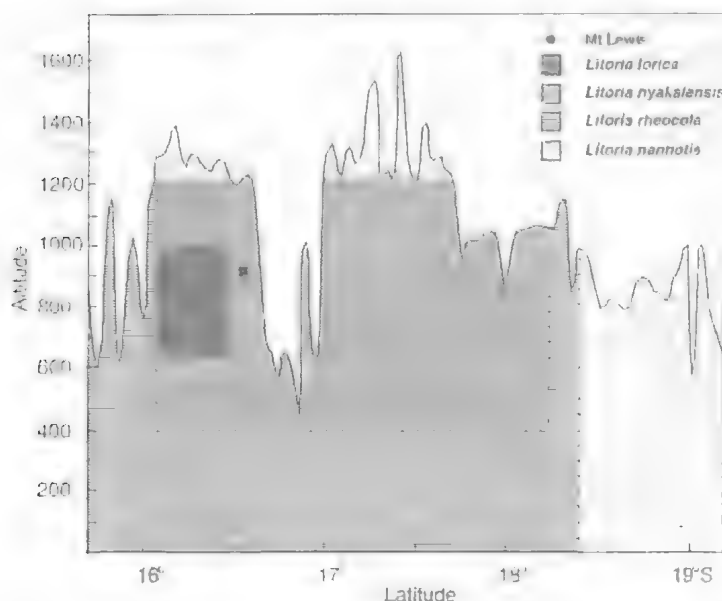


FIG. 1. Schematic profile of the Wet Tropics showing altitudinal and latitudinal range of Torrent Treefrog species and location of Mt Lewis Rd.

present south of the Herbert River to the Blue-water Range (146°27'E, 19°11'S) (Covacevich & McDonald, 1993; Fig. 1). In the last decade, all Torrent Treefrog species have undergone catastrophic declines, particularly upland populations (> 300m), and these frogs are no longer found in many former localities (Richards et al., 1993; McDonald & Alford, 1999). All four species are formally listed as 'Endangered' under Queensland and Commonwealth legislation.

Although Liem (1974) and Davies & McDonald (1979) carefully described differences among Torrent Treefrogs, and provided keys, there is still confusion over the identification of *lorica* and *nyakalensis*. Photos, pictures and descriptions in field guides are inconsistent and may be misleading (Hero 1996a). For example, a photo labelled *nyakalensis* in Nix & Switzer (1991: 94) appears to be *rheocola* and the painting Nix & Switzer (1991: 92) inaccurately depicts *lorica* colouration and micro-habitat; in Tyler (1992: 26, 32), a photo of *nyakalensis* appears to be *rheocola* and vice versa; in Cogger (1992: 144), a photo from Windsor Tableland is labelled *lorica*; this photo is again labelled *lorica* in Barker et al. (1995: 137), but is emended to *rheocola* in Cogger (2000), the photo of *nyakalensis* in Hero & Fickling (1994: 144) may be *rheocola*. It seems that there are few published

photographs of *nyakalensis* (but see Barker et al., 1995: 139; Tyler, 1992: 32; Queensland Parks & Wildlife Service, 2000; McDonald, 2000: 180), and no photographs of *lorica* are known.

Evolutionary relationships within *Litoria* are poorly resolved but morphological (Tyler, 1982) and immunological (Hutchinson & Maxson, 1987) comparisons suggest that the Torrent Treefrog radiation is independent of other torrent-adapted hylids in Australia and New Guinea, and is therefore an important component of phylogenetic diversity in Hylidae. Within Torrent Treefrogs the ecologically similar species pairs (*nannotis*, *lorica*) and (*rheocola*, *nyakalensis*) share morphological features and are difficult to distinguish from one-another (Davies & McDonald, 1979). Liem (1974), however, regarded *rheocola* as

the 'ancestral stock' and presented a phylogenetic hypothesis with *nyakalensis* sister group to *nannotis*.

The primary aim of this paper is to clarify differences among Torrent Treefrogs and to provide a revised guide for field identification. Secondly, I use these differences to reconstruct a phylogeny of this group. I compare this phylogeny against mitochondrial DNA divergence within and between *nannotis*, *rheocola* and outgroup species. Only formalin fixed museum specimens are available from *nyakalensis* or *lorica*, so it is difficult to address Liem's hypothesis with DNA sequence data, or to determine genetic divergence among sister species. Thirdly, I refer museum specimens from the Carbine Uplands to *lorica* and report the last sighting in the wild of this species.

COMPARISONS AMONG TORRENT TREEFROGS

Existing primary literature reports 44 differences among Torrent Treefrogs (Liem, 1974; Davies & McDonald, 1979; Richards, 1992; Hodgkison & Hero, 2002). These include 12 internal structures, and 14 ecological, behavioural, developmental, colouration or geographical differences (reviewed above) which could not be scored from preserved specimens. Type

collections in the Queensland Museum, including holotypes of *lorica*, *nyakalensis* and *rheocola*, along with additional specimens, were examined for the remaining 21 aspects of external morphology. Specimens were also measured for 10 morphometric traits following (Tyler, 1968) and (Alford et al., 1999): Snout-Vent length, SV; Tibial Length, TL; Forearm Length, FL; Interlimb Length, IL, from axilla to groin; Head Width, HW; Head Length, HL; InterNasal distance, IN; Eye - Nasal distance, EN; Eye Diameter, ED; Tympanum - Nasal distance, TN, from the anterior edge of the tympanum to the posterior edge of the nostril. Specimens examined are given in appendix.

Differences among Torrent Treefrog species (Table 1) include aspects of external morphology, features 1-14, which are grouped as a key and listed, within each group, according to ease of use in the field. Features 1-6 separate the ecological pairs, (*nannotis* + *lorica*) from (*nyakalensis* + *rheocola*). Features 7-12 separate *nyakalensis* from *rheocola*. Features 13 and 14 separate *nannotis* from *lorica*. Morphometric ratios incorporating SV, TL, FL, HW and HL measurements (features 29-31) show strong differences in mean values but overlap in range, and should be used as corroborative evidence in identification. Features 23-28 are colouration, larval and behavioural traits applicable to live specimens or preserved tadpoles (see Richards, 1992 for a tadpole key). Features 15-22 are osteological which generally require cleared-and-stained specimens or skeletal preparations, but may also be visible in X-ray radiographs. Features 7 and 12 include both external appearance and associated osteological features, which are not essential to field identification but add resolution to species discrimination. For example in character 7, thumbs of *nannotis* and *lorica* are similar in external appearance but differ internally in the number of metacarpal flanges, conversely, the enlarged prepollex of *lorica* and the flattened, conical thumb of *nyakalensis* differ externally but are osteologically similar (Davies & McDonald, 1979).

Species differ particularly in head shape, webbing, size and secondary sexual characteristics. *Litoria nannotis* and *lorica* have short, broad heads ($HW/SV > 0.35$; $HL/HW < 1.01$) with a rounded canthus rostralis and concave loreal area. *Litoria lorica* has a truncate snout, when viewed from above or in profile, with the nostrils virtually at the tip. *Litoria nyakalensis* and *rheocola* are more gracile ($HL/SV < 0.36$;

$HL/HW > 0.93$) with *nyakalensis* somewhat intermediate between the relatively angular head and protruding snout of *rheocola* and the rounded head and snout of *nannotis*. This difference is difficult to characterise but may be seen in ventral view where the triangular snout of *rheocola* protrudes beyond the margin of the mandible, whereas the margin of the snout of *nyakalensis* tends to approximate the jaw line. Torrent Treefrogs have sparsely webbed fingers and near fully webbed toes. Although webbing varies within species (Davies & McDonald, 1979) there are also consistent differences between species and these are the most useful characters for separating female *rheocola* from female *nyakalensis*. In most *rheocola* specimens webbing reaches the second-subarticular tubercle at the end of the first phalanx, measured on the outer edge of the third finger (Fig. 2A). In *nannotis*, *lorica* and *nyakalensis* hand-webbing is less extensive and rarely extends more than half-way along the first phalanx (Fig. 2B). One *nyakalensis* specimen (J29287 from Mt Lewis Rd) has extensive finger-webbing, but agrees with *nyakalensis* in other respects. In *nannotis*, *lorica* and *rheocola* webbing along the fifth toe extends to intercalary element or disc (Fig. 2C), whereas *nyakalensis* has slightly reduced toe-webbing, which does not extend $>2/3$ along the first phalanx of the fifth toe (Fig. 2D).

Litoria nannotis is larger than other Torrent Treefrogs, and body-size varies geographically in this species. The Carbine Tableland population comprises very large individuals (male SV 54-60mm, Mt Lewis Rd, Fig. 1) whereas remaining populations range from 40-53mm in male SV (pers. obs., I shall discuss the status of the Carbine population elsewhere). Other species are smaller and similar to each other in size, but there is considerable variation in *nyakalensis*, males 30-31mm SV among type specimens, from the southern Atherton Tableland, and males up to 41mm SV from other areas. Males of *nannotis*, *lorica* and *nyakalensis* have robust, enlarged arms, evident in sexual dimorphism for relative limb length (FL/TL males $>$ females, Table 1). *Litoria rheocola* does not have enlarged arms and differs from *nyakalensis* males on this ratio (male FL/TL , *nyakalensis* $>$ *rheocola*, Table 1). Mature male *lorica* and *nannotis* have accessory spines on the chest, and develop further spines around the jaws and legs during the breeding season. In males of these species the proximal $2/3$ of the thumb, around the prepollex, is enlarged up to three times the base thumb width and the dorsal

TABLE 1. Morphological variation in Torrent Treefrogs.

Feature	<i>Litoria nannotis</i>	<i>Litoria lorica</i>	<i>Litoria nyakalensis</i>	<i>Litoria rheocola</i>
1. Accessory spinules on chest, limbs and face (♂♂)	Present (a)	Present (a)	Absent (b)	Absent (b)
2. Tympanic annulus	Indistinct or obscured (a)	Indistinct or obscured (a)	Distinct (b)	Distinct (b)
3. Expansion of discs on fingers 2, 3, 4, cf. finger-width at base of discs	Large, > 2 × finger-width (a)	Large, > 2 × finger-width (a)	Moderate, < 2 × finger-width (b)	Moderate, < 2 × finger-width (b)
4. Canthus rostralis in cross section, horizontal curvature	Rounded, indistinct, moderately curved (a)	Rounded, moderately curved (a)	Distinct, ± angular, pronounced curvature (b)	Sharp, angular ridge, ± straight or only slightly curved (b)
5. Loreal curvature in cross-section	Distinctly concave (a)	Strongly concave (a)	Slightly concave (b)	Not or only slightly concave (b)
6. Snout length (horizontally from eye to tip-of-snout)	Shorter than eye diameter (a)	Shorter than eye diameter (a)	Longer than eye diameter (b)	Longer than eye diameter (b)
7. Prepollex and thumb, bony flanges on the first metacarpal (♂♂) (ordered: a-b-c)	Greatly enlarged for proximal 2/3, multiple metacarpal flanges (a)	Greatly enlarged for proximal 3/4, single metacarpal flange (b)	Enlarged to terminal disc, conical appearance, single metacarpal flange (b)	Not enlarged, no metacarpal flange (c)
8. Nuptial pad, dorsal surface of thumb and prepollex (♂♂) (ordered: a-b-c)	Large, dense covering of coarse spines (a)	Large, dense or sparse covering of coarse spines (a)	Large (> 1/2 thumb; gap < thumb-width between nuptial pad and disc), coarse spines (a)	Small (< 1/2 thumb; gap > thumb-width to disc), oval pad of fine spines (b)
9. Terminal disc on thumb, cf. width at base of disc	Distinctly wider than thumb (a)	Distinctly wider than thumb (a)	Reduced, ± thumb width (b)	Distinctly wider than thumb (a)
10. Hand webbing along the outer margin of the longest finger (between fingers 3 & 4)	0-3/5 length of proximal phalanx (average 1/5) (a)	1/3-2/3 proximal phalanx (average 1/2) (a)	0-1/1 (complete length of proximal phalanx)* (average 1/3) (a)	1/2-1/1 (complete length of proximal phalanx) (average 4/5) (b)
11. Foot webbing along the inner margin of shortest toe, (between toes 1 & 2)	1/2-1/1 along proximal phalanx to disc (average >4/5) (a)	1/1, complete, reaches base of disc (all specimens 1/1) (a)	0-3/4 along the proximal phalanx (average 1/3) (b)	3/4-1/1, from end of proximal phalanx to disc (average >4/5) (a)
12. Forearm width, bony flanges on humerus (♂♂) (Davies & McDonald 1979, fig. 5)	Robust, pronounced dorsal and ventral humeral flanges (a)	Robust, moderate humeral flanges (a)	Robust, moderate humeral flanges (a)	Slight, no flanges (b)
13. Adult body size	Large, SV > 40mm (average: ♂ 48mm, ♀ 51mm) (a)	Moderate, SV < 40mm (average: ♂ 33mm, ♀ 34mm) (b)	Moderate, SV < 41mm (average: ♂ 35mm, ♀ 36mm) (b)	Moderate, SV < 40mm (average: ♂ 31mm, ♀ 35mm) (b)
14. Snout shape, position of nostrils relative to tip-of-snout and end-of-mouth, in profile view	Bluntly rounded, nostrils slightly posterior to snout, ± level with mouth (a)	Truncate, nostrils ± terminal, slightly anterior to mouth (b)	Bluntly rounded to pointed, nostrils posterior to snout and mouth (a)	Bluntly pointed, nostrils posterior to snout, ± level with mouth (a)
15. Nasals - sphenethmoid	In contact (a)	Separated (b)	Overlapping (a)	Overlapping (a)
16. Frontoparietal fontanelle	Elongate, length > 3 × width (a)	Elongate, length > 3 × width (a)	Oval, length < 3 × width (b)	Oval, length < 3 × width (b)
17. Ossification of medial prootic	Robust, complete (a)	Incomplete (b)	Robust, complete (a)	Robust, complete (a)
18. Quadratojugal	Complete, articulating with squamosal (a)	Complete, articulating with squamosal (a)	Incomplete, does not contact squamosal (b)	Incomplete, does not contact squamosal (b)
19. Preorbital process on pars facialis of maxillary	Present (a)	Absent or indistinct (b)	Absent or indistinct (b)	Absent or indistinct (b)
20. Alary processes of premaxillae, in dorsal view	Not projecting beyond jawline (a)	Projecting forward beyond jawline (b)	Projecting forward, beyond jawline (b)	Projecting forward, beyond jawline (b)
21. Dentigerous processes of prevomers	Truncate, 4-5 teeth (a)	Moderate, 6-7 teeth (b)	Short, 4-6 teeth (a)	Short, 4-6 teeth (a)
22. Intercalary elements	Cartilage (a)	Cartilage (a)	Bone (b)	Bone (b)
23. Dorsal head colouration (live)	Similar to dorsum, mottled slate (a)	Similar to dorsum, uniform or mottled (a)	Similar to dorsum, uniform or mottled (a)	Conspicuous lighter triangle from interorbital to snout (b)
24. Ventral colouration (live)	Cream (a)	Cream (a)	Cream, pink flush (b)	Cream (a)
25. Iris colouration (live)	Silver to golden (a)	Silver to golden (a)	Golden or sandy to brown, not reddish (a)	Dark red to russet brown (b)
26. Larval colouration	Diffuse dark pigment on tail and fins, fins yellow tinged with yolk cells	Unknown	Discrete, dark blotches on cream tail and clear fins	Diffuse dark pigment on tail, clear, sparsely pigmented fins
27. Larval oral papillae on anterior upper labium	Two or more complete rows	Unknown	One complete row	One complete row
28. Call (♂)	Deep 'crawk, crawk, crawk' and quiet popping	Unknown	Rasping, slow growl	Harsh, repetitious 'wreck'
29. Head shape (HL/HW), Range; mean ♂, mean ♀	Range: 0.87-1.01 ♂: 0.93, ♀: 0.94	Range: 0.89-0.95 ♂: 0.92, ♀: 0.92	Range: 0.93-1.04 ♂: 1.01, ♀: 1.00	Range: 0.94-1.11 ♂: 1.04, ♀: 1.00
30. Limb ratio (FL/TL), Range; mean ♂, mean ♀	Range: 0.37-0.51 ♂: 0.46, ♀: 0.43	Range: 0.40-0.55 ♂: 0.47, ♀: 0.45	Range: 0.44-0.55 ♂: 0.50, ♀: 0.46	Range: 0.40-0.47 ♂: 0.44, ♀: 0.44
31. Relative head-width (HW/SV), Range; mean ♂, mean ♀	Range: 0.35-0.42 ♂: 0.37, ♀: 0.36	Range: 0.33-0.38 ♂: 0.37, ♀: 0.34	Range: 0.31-0.36 ♂: 0.33, ♀: 0.33	Range: 0.32-0.34 ♂: 0.33, ♀: 0.33

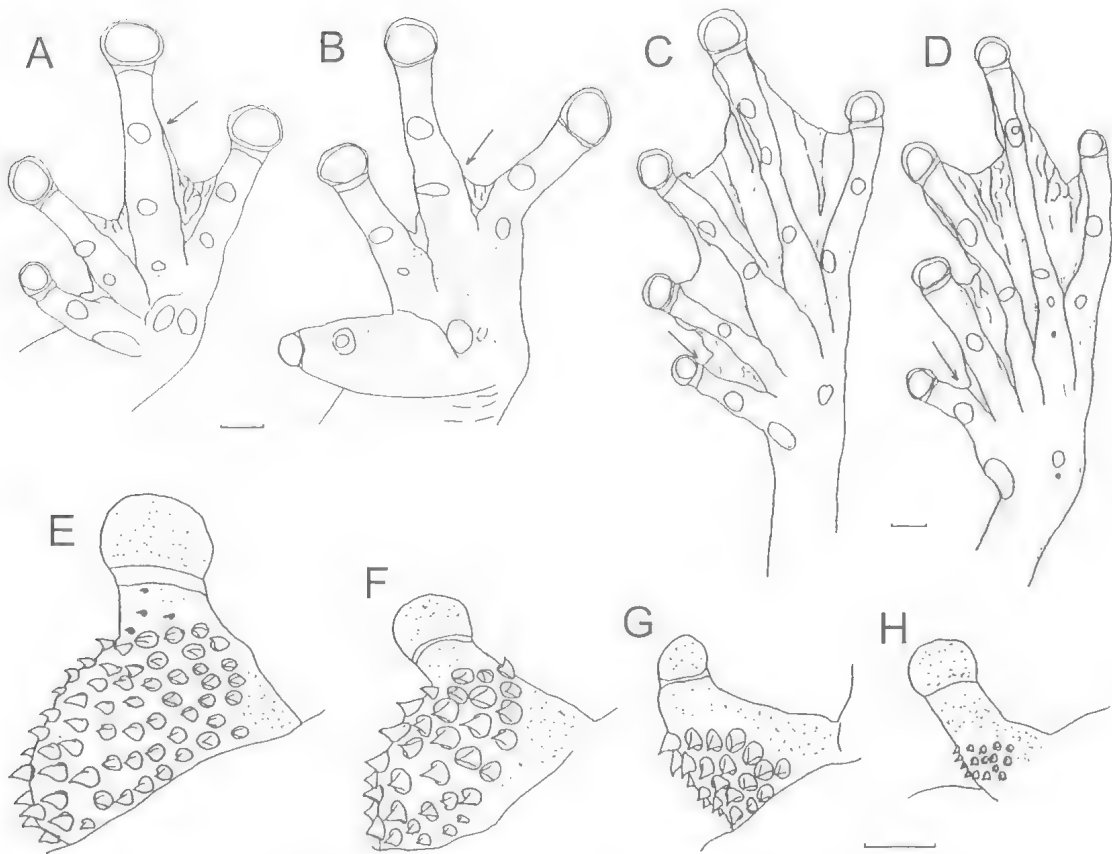


FIG. 2. Differences among Torrent Treefrogs in: Hand-webbing: A, *rheocola* J22631; B, *nyakalensis* J22624. Foot-webbing: C, *rheocola* J22631; D, *nyakalensis* J22624. Thumb shape and nuptial pad: E, *nannotis* J52965; F, *lorica* J36090; G, *nyakalensis* J22624; H, *rheocola* J22631. Arrows show differences in hand and foot-webbing between *rheocola* and *nyakalensis*. Scale bars: 1mm.

surface is covered in coarse nuptial spines. This part of the thumb is also enlarged in females, up to twice the base thumb width, but the distal third of the thumb is not enlarged in either sex (Fig. 2E, F). By contrast, in male *nyakalensis* the thumb is enlarged up to the disc, which is reduced in size, giving the thumb a conical appearance (Fig. 2G). Coarse nuptial spines cover most of the dorsal surface of the male *nyakalensis* thumb and the gap between this nuptial pad and the disc is less than the thumb width at the base of the disc (Fig. 2G). Female *nyakalensis* do not have an enlarged thumb, spines or enlarged arms, and closely resemble female *rheocola*. *Litoria rheocola* does not have enlarged thumbs and males have a small, oval, finely spinose nuptial pad on the prepollex, which is separated from the thumb disc by more than the base thumb width (Fig. 2H).

No other morphometric ratios or measurements gave significant separation among species. Liem (1974) suggested IN/EN as a diagnostic separating *nyakalensis* (> 0.98) from *nannotis* and *rheocola* (< 0.97). These variables are error prone and this ratio is inconsistent (Davies & McDonald, 1979), indeed, Liem's measurements misdiagnose the holotype of *nyakalensis* (IN/EN = 0.91). Nevertheless, on the limited samples considered here, IN/EN separated female *nyakalensis* (1.01-1.14) from female *rheocola* (0.93-0.96). The alternative ratio (HL/HW), suggested by Davies & McDonald (1979), gave similar mean values in both species. Liem (1974) noted a single outer metacarpal tubercle in *nannotis* and paired tubercles in *nyakalensis* and *rheocola* but this feature is often indistinct or grades within species from a single tubercle with two confluent lobes to paired tubercles. An inner

tarsal fold is present in all species but this varies from distinct to indistinct or absent within some *lorica* and *nyakalensis* specimens (cf. Liem, 1974, 'absent in *nyakalensis*'). Male *nannotis* do call (cf. Liem, 1974), although more commonly they may use other modes of communication (Torr, 1994). All species have a small tympanum which is covered with skin and varies with specimen preservation (Czechura et al., 1987), but the tympanic annulus is generally less distinct in *nannotis* and *lorica*.

PHYLOGENETIC ANALYSIS

Phylogenetic trees were derived using parsimony and outgroup rooting, with exhaustive searches in PAUP*4.01 (Swofford, 1998). The intent of this analysis is to examine morphological change within the group, not to challenge its monophyly, which was forced as a constraint on analyses. Previous phylogenetic analyses suggest that the *Citropa* group (represented here by *Litoria pearsoniana*) is a sister to the Torrent Treefrogs, and that the *Eucnemis* group (*Litoria serrata*) and *Lesueuri* group (*Litoria lesueuri*) are basal to this clade (Hutchinson & Maxson, 1987). Tyler & Davies (1979) suggest a phylogenetic association between *Nyctimystes dayi*, Torrent Treefrogs and the *Eucnemis* group. Representatives from each of these species groups were examined and scored as outgroups (Appendix). The dataset consists of characters 1-25 in Table 1 and nine additional characters which do not vary among Torrent Treefrogs (Table 2) (character, states a/b: 26, fringes along toes absent/present; 27, vocal sac absent/present; 28, ovarian eggs large, >1.5 mm/small, <1.5 mm diameter; 29, eggs unpigmented/pigmented; 30, larvae suctorial/non-suctorial; 31, larval tooth rows complete/incomplete; 32, larval papillae fully surround oral disk/anterior gap in papillae; 33, larval anal tube medial/dextral; 34, tympanum small, <5% SV/large, >5% SV). Characters seven and eight were ordered, with a single flange on the first metacarpal considered intermediate between no flange and multiple flanges (character 7), and finely spinose nuptial pads intermediate between non-spinose and coarsely spinose pads (character 8). All other characters were unordered. Photographs and field observations were used to corroborate scoring of external features and colouration. The yellow-tinged venter of male *lesueuri* and dark iris of *N. dayi* were considered unique, uninformative states (characters 24, 25; state c). Scoring of osteological characters was

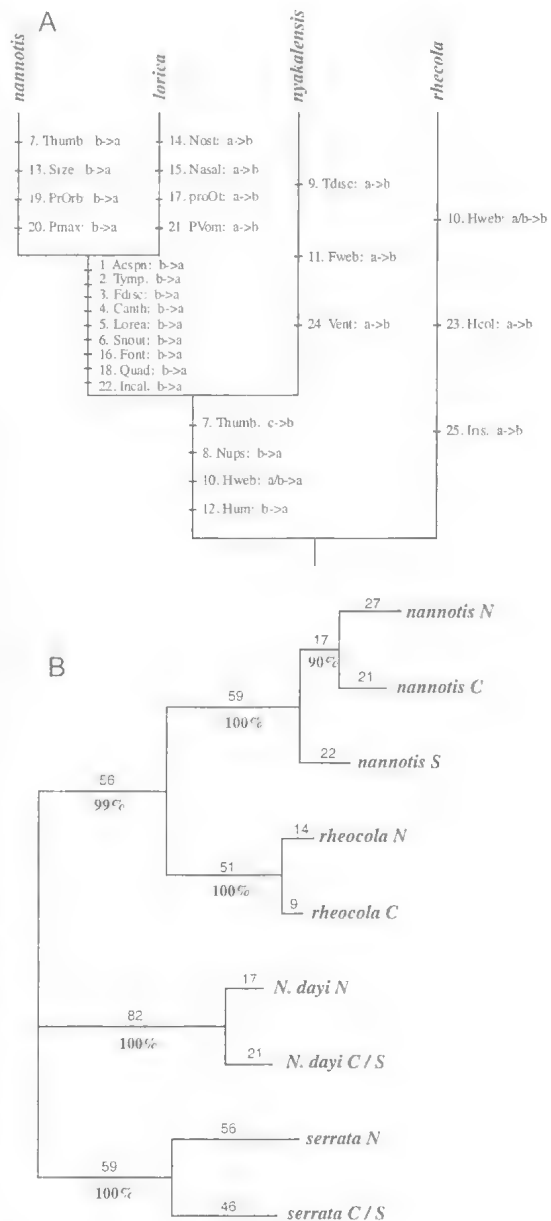


FIG. 3. A, phylogeny of Torrent Treefrogs based on 34 morphological characters showing state-changes along branches. Outgroups *serrata*, *lesueuri*, *pearsoniana* and *N. dayi* are not shown. B, mitochondrial DNA phylogeny among species and intraspecific lineages of *nannotis*, *rheocola*, *serrata* and *N. dayi*, from combined fragments of 16S (500bp) and cytochrome *b* (530bp) genes. Branch lengths are shown along with percentage bootstrap support. N = Northern, C = Central and S = Southern Wet Tropics.

based on published descriptions (Tyler & Davies, 1978; Davies & McDonald, 1979; McDonald & Davies, 1990) and cleared and stained specimens of *serrata*, with corroboration from related species (Eucnemis group: Tyler & Davies, 1979; Tyler et al., 1986). Tadpole characters were taken from the literature (Liem, 1974; Davies, 1989; Davies & Richards, 1990; McDonald & Davies, 1990; Richards, 1992; Anstis et al., 1998) and scored as ambiguous in *lorica*.

The single shortest tree, 60 steps, is identical in topology to Liem's (1974) hypothesis, with *rheocola* basal within Torrent Treefrogs (Fig. 3A). This tree differs from Liem's analysis in character support. Of the nine characters examined by Liem (1974), three are considered uninformative here (inner tarsal fold, outermetacarpal tubercle, male call), for reasons discussed above, and a further three are interpreted differently (the distinct tympanum and angular canthus rostralis are qualitatively similar in *nyakalensis* and *rheocola*, although these differ in degree, and the enlarged prepollux of male *nyakalensis* differs from *rheocola* cf. Liem, 1974). The consistency index for the tree is 0.63 and the retention index 0.58 with no homoplasy in ingroup comparisons. Within the constrained search space of 225 trees there were no 61 step trees and four 62 step trees (2 steps longer), one of which gave an alternate topology with *nyakalensis* and *rheocola* as sister species. The clade (*nyakalensis*, *lorica*, *nannotis*) is uniquely supported by enlarged thumbs with metacarpal flanges, coarsely spinose nuptial pads, and robust arms with humeral flanges (Fig. 3A). No unique character states support the competing hypothesis (*nyakalensis* + *rheocola*). When the constraint of ingroup monophyly was relaxed 10,395 trees were searched and two further 60-step trees were discovered, with *N. dayi* either as sister to *rheocola* or sister to *nannotis* + *lorica*. The close association of *N. dayi* with Torrent Treefrogs is supported by egg, larval and adult characters (large, unpigmented eggs; suctorial tadpoles with a median anal tube; tympani obscured by skin) which may be adaptations to torrent streams. Monophyly of Torrent Treefrogs is supported by a unique morphological trait; spinose nuptial pads.

Although data were not obtained from *nyakalensis* or *lorica*, mitochondrial DNA sequences from *nannotis* and *rheocola* are consistent with current understanding of Torrent Treefrogs (Fig. 3B). 16S and COI sequences were obtained from geographically separated lineages of *nannotis*, *rheocola*, *serrata* and *N. dayi*, in the Northern (N), Central (C) and/or Southern Wet Tropics (S). These samples represent the maximum divergence within each species. Genbank accession numbers are (COI, 16S: *nannotis* N AF304236, AF136325; C AF304243, AF136323; S AF304259, AF136322; *rheocola* N AF304283, AF136327; C AF304293, AF136326; *serrata* N AF304221, AF136299; C/S AF304222, AF136297; *N. dayi* N AF304268, AF136329; C/S AF304266, AF136328). Sequences were aligned by eye with alignment gaps in 16S treated as ambiguous states. The combined sequences (500bp 16S + 530bp COI) were analysed using an exhaustive parsimony search and 1000 bootstrap reanalyses in PAUP*4.01 (Swofford, 1998). The shortest tree, with 557 steps, is shown in Fig. 3B. There is strong support for *nannotis* + *rheocola* (100% bootstrap) and negligible support for other interspecific groupings, in this limited comparison. The shortest tree conflicting with this *nannotis* + *rheocola* clade was 575 steps (18 steps longer). Divergence within *nannotis* and *rheocola* is from one half to one eighth that between these species. Applying rough estimates of divergence rates, around 2% per million years for mitochondrial protein coding genes (Moritz, Dowling & Brown, 1987) and around 1% per million years for the ribosomal 16S gene (Caccone et al., 1997), to mean divergences between *nannotis* and *rheocola* (19.7% at COI and 10.4% at 16S, using HKY 85 distances from

TABLE 2. Phenotypic character state matrix. Character states in *nannotis* are coded 'a', with alternative states 'b' and 'c'. Characters 7 and 8 are ordered (a b c).

Character	12345678911111111112222222222233333 0123456789012345678901234
<i>nannotis</i>	aaaaaaaaaaaaaaaaaaaaaaaaaaaaaaaaaaaaa
<i>lorica</i>	aaaaaabaaaaabbbababbbbaaaaaa????a
<i>nyakalensis</i>	bbbbbbbababababababbbbababaaaaa
<i>rheocola</i>	bbbbbbcbababbaababbbabbabaaaaa
<i>Nyctimystes</i>	babbabccababbaababbabaaacbbaaaaa
<i>pearsoniana</i>	bbbbbbccaabbbbaababbabaaaabbbbbba
<i>genimaculata</i>	bbababccababaaabaaaaaaaababbbbbbb
<i>lesueuri</i>	bbbbbbccbabbaaabaabaacaaabbbbaabb

PAUP*) suggests a mid-Miocene split within Torrent Treefrogs compared with roughly Pliocene splits among lineages within *nannotis* (COI 7.1–11.2%; 16S 2.2–2.4%), and Pleistocene divergence within *rheocola* (COI 3.3%; 16S 1.3%). The discrepancy in ratios of these values indicates that interspecific divergences are underestimates, particularly at COI, due to site saturation and rate variation among nucleotide sites.

GEOGRAPHIC DISTRIBUTION OF *LITORIA LORICA*. Several misclassified individuals were discovered among the specimens examined including one *N. dayi* registered as *nyakalensis*, and two *serrata*, two *nyakalensis* and one *lorica* registered as *nannotis*. In addition, a search of the combined USA herpetological collection register (www.calacademy.org/research/herpetology/Comb_Coll_Index) revealed further specimens registered as *lorica* in the University of Michigan collection (UMMZ). These *lorica* specimens are of particular interest as they extend the known range of this enigmatic species. QMJ42235, is a mature male with densely spinose nuptial pads and accessory spines on the chest, jaws and legs. The size (32.3mm SV) and truncate snout distinguish QMJ42235 from mature *nannotis* and there are no notable differences between this individual and *lorica* type specimens. Thirteen specimens from the University of Michigan were similarly consistent with *lorica*, but not with *nannotis*. At present *lorica* is known from only three sites on the Thornton uplands (Table 3). The maximum straight line distance between sites is approximately 10 km. Two of these are published records, from streams flowing off Thornton Peak into the Bloomfield and Daintree Catchments (Davies & McDonald, 1979; McDonald, 1992). The third is a personal observation at Roaring Meg Creek, below Mt Pieter Botte, from 3–5 December 1991. Numerous *lorica* (>12 individuals) were observed at night clustered in the splash-zone of a major cascade, and also in deep cracks beside this cascade during the day (DM Hillis, M Cunningham, C Moritz, pers.

obs.). Several *nannotis* were present at this cascade and at other points along the stream, and these two species were clearly distinguished by size. This appears to be the last observation of *lorica* in the wild. Other declining species (*rheocola* and *Taudactylus acutirostris*) were observed at the same locality at this time. I saw a single female *nannotis* at the same site on 5–6 April 1993, and none of these species was found during searches in November 1994 and 11–12 June 1995. Trennery (1994) attributed a torrent tadpole found in surveys of Roaring Meg Ck (23–24 August 1993) to *nannotis* but it is also conceivable that this was *lorica*, the tadpole of which is unknown.

Specimen QMJ42235 was collected by G. Montieth, D. Yeates and G. Thompson on 2 November 1983, on an unnamed tributary of the Mossman River which crosses the Mossman Bluff track at around 900m altitude. The UMMZ specimens were collected in the same area, '3.5 miles west of Mossman near vertical rock faces in turbulent stream bed', by J. Bailey on the 19 August 1971. These sites increase the linear range of *lorica* to 46km, with a total extent of 120km². More importantly, these records extend the range of *lorica* to a second upland rainforest area, the Carbine Tableland approximately 34km south of the type locality. Although all four Torrent Treefrogs have undergone sudden declines, the geographically restricted upland species, *lorica* and *nyakalensis*, have not been observed since December 1991 (above) and November 1990 (Hero & Fickling, 1994), respectively, despite ongoing monitoring and searches of historically known sites (Richards, et al., 1993; Trennery, et al., 1994; Hero, 1996b; Williams & Hero, 1998; Hero et al. 1998; McDonald & Alford, 1999). *Litoria lorica* and *nyakalensis* fulfil all criteria for listing as 'Critically Endangered' under the Commonwealth *Environment Protection and Biodiversity Conservation Act (1999)*, these being: severe declines, very restricted distribution, very low estimated population size and high probability of extinction from further declines. Recent

TABLE 3. Records and distribution of *Litoria lorica*. * see text for further details.

Site	Latitude	Longitude	Altitude	Year	Reference
Roaring Meg Ck	145°25'E	16°04'S	680m	1991	Pers. obs.*
Alexandra Ck	145°21'E	16°07'S	640m	1976	Davies & McDonald, 1979
Hilda Ck	145°23'E	16°10'S	1,000m	1990	Covacevich & McDonald, 1993
Mossman Gorge	145°17'E	16°28'S	?	1971	J. Bailey (UMMZ register)*
Mossman Gorge	145°17'E	16°28'S	900m	1983	G. Montieth, pers. comm.*

publications report the rediscovery of two other upland rainforest frogs, *Taudactylus rheophilus* and *Taudactylus acutirostris*, as small, isolated populations in the central and northern Wet Tropics, including Mt Lewis (Marshall, 1998; Hero et al. 1998). Increasing search effort has also resulted in the discovery of upland populations of *nannotis* and *rheocola* which may have been previously overlooked (Hero et al. 1998; McDonald pers. comm.). These discoveries fuel hope that remnant populations of *lorica* and *nyakalensis* remain to be discovered in the Wet Tropics. Rediscoveries of other species on the Carbine Tableland, together with these new records, suggest an urgent need for intensive surveys across the entire Thornton and Carbine uplands.

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LITERATURE CITED

- ALFORD, R., BRADFIELD, K. & RICHARDS, S. 1999. Measuring and analysing developmental instability as a tool for monitoring frog populations. Pp. 34-43. In Campbell, A. (ed.) Declines and disappearances of Australian frogs. (Environment Australia: Canberra).
- ANSTIS, M., ALFORD, R.A. & GILLESPIE, G.R. 1998. Breeding biology of *Litoria booroolongensis* (Moore, 1961), and *Litoria lesueuri* (Duméril & Bibron, 1841) (Anura: Hylidae) and comments on population declines of *booroolongensis*. Transactions of the Royal Society of South Australia 122(1): 33-43.
- BARKER, J., GRIGG, G.C. & TYLER, M.J. 1995. A field guide to Australian frogs. (Surrey Beatty & Sons: Sydney).
- CACCONI, A., MILINKOVITCH, M., SBORDONI, V. & POWELL, J. 1997. Mitochondrial DNA rates and biogeography in European newts (genus *Euproctus*). Systematic Biology 46(1): 126-144.
- COGGER, H.G. 1992. Reptiles and amphibians of Australia. 5th Ed. (Reed Books: Sydney).
2000. Reptiles and amphibians of Australia. 6th Ed. (Reed Books: Sydney).
- COVACEVICH, J. & McDONALD, K.R. 1993. Distribution and conservation of frogs and reptiles of Queensland rainforests. Memoirs of the Queensland Museum 34(1): 189-199.
- CZECHURA, G.V., INGRAM, G.L. & LIEM, D.S. 1987. The genus *Nyctimystes* (Anura: Hylidae) in Australia. Records of the Australian Museum 39: 333-338.
- DAVIES, M. 1989. Developmental biology of the Australopapuan hylid frog *Litoria eucnemis* (Anura: Hylidae). Transactions of the Royal Society of South Australia 113(4): 215-220.
- DAVIES, M. & McDONALD, K.R. 1979. A new species of stream-dwelling hylid frog from northern Queensland. Transactions of the Royal Society of South Australia 103(7): 169-176.
- DAVIES, M. & RICHARDS, S. 1990. Developmental biology of the Australian hylid frog *Nyctimystes dayi* (Günther). Transactions of the Royal Society of South Australia 114(4): 207-211.
- HERO, J.-M. 1996a. Corrections to identification of photographs of 'endangered' frogs of the wet tropics rainforest. Herpetofauna 26: 32.
- 1996b. Where are Queensland's missing frogs? Wildlife Australia 32(2): 8-12.
- HERO, J.-M., HINES, H., MEYER, E., MORRISON, C., STREATFIELD, C. & ROBERTS, L. 1998. New records of 'declining' frogs in Queensland, Australia. Froglog 29: 1-4.
- HERO, J.-M. & FICKLING, S. 1994. A guide to stream-dwelling frogs of the Wet Tropics Rainforests. (James Cook University of North Queensland: Townsville).
- HODGKISON, S. & HERO, J.-M. 2001. Daily behaviour and microhabitat use of the Waterfall Frog, *Litoria nannotis* in Tully Gorge, eastern Australia. Journal of Herpetology 35: 116-120.
2002. Seasonal behaviour of *Litoria nannotis*, *L. rheocola* and *Nyctimystes dayi* in Tully Gorge, north Queensland, Australia. Pp. 34-51. In Natrass, R. (ed.) 'Frogs in the Community' - proceedings of the Brisbane conference 13-14 Feb. 1999. (Queensland Frog Society Inc.: Brisbane).
- HUTCHINSON, M. & MAXSON, L. 1987. Phylogenetic relationships among Australian tree frogs (Anura: Hylidae: Pelodryadinae): an immunological approach. Australian Journal of Zoology 35: 61-74.
- LIEM, D.S. 1974. A review of the *Litoria nannotis* species group, and a description of a new species of *Litoria* from northern Queensland, Australia (Anura: Hylidae). Memoirs of the Queensland Museum 17: 151-168.

- MARSHALL, C. 1998. The reappearance of *Taudactylus* (Anura: Myobatrachidae) in north Queensland streams. *Pacific Conservation Biology* 4: 39-41.
- MCDONALD, K.R. 1992. Distribution patterns and conservation status of North Queensland rainforest frogs. (Queensland Department of Environment and Heritage and Wet Tropics Management Agency: Cairns).
2000. Frogs. Pp. 171-174. In Ryan, M. & Burwell, C. (eds) *Wildlife of Tropical North Queensland*. (Queensland Museum: Brisbane).
- MCDONALD, K.R. & ALFORD, R.A. 1999. A review of declining frogs in northern Queensland. Pp. 14-22. In Campbell, A. (ed.) *Declines and disappearances of Australian frogs*. (Environment Australia: Canberra).
- MCDONALD, K.R. & DAVIES, M. 1990. Morphology and biology of the Australian tree frog *Litoria pearsoniana* (Copland) (Anura : Hylidae). *Transactions of the Royal Society of South Australia* 114: 145-156.
- MORITZ, C., DOWLING, T. & BROWN, W. 1987. Evolution of animal mitochondrial DNA: relevance for population biology and systematics. *Annual Review of Ecology and Systematics* 18: 269-292.
- QUEENSLAND PARKS & WILDLIFE SERVICE 2000. Declining frogs of Australia's Wet Tropics rainforests. State of Queensland pamphlet BP1235-1.
- NIX, H.A. & SWITZER, M. 1991. Rainforest animals. Atlas of vertebrates endemic to Australia's Wet Tropics. Kowari 1. (Australian National Parks and Wildlife Service: Canberra).
- RICHARDS, S.J. 1992. The tadpole of the Australian torrent frog *Litoria nyakalensis* (Anura, Hylidae), and a key to the torrent tadpoles of northern Queensland. *Alytes* 10: 99-103.
- RICHARDS, S.J., MCDONALD, K.R. & ALFORD, R.A. 1993. Declines in populations of Australia's endemic tropical rainforest frogs. *Pacific Conservation Biology* 1: 66-76.
- SWOFFORD, D.L. 1998. PAUP*. Phylogenetic Analysis Using Parsimony (*and other methods). Version 4. (Sinauer Associates Inc: Sunderland, Massachusetts).
- TORR, G. 1994. When a wave's as good as a wink. *Wildlife Australia* 31(4): 32.
- TRENNERY, M., LAURANCE, W. & MCDONALD, K.R. 1994. Further evidence for the precipitous decline of endemic rainforest frogs in tropical Australia. *Pacific Conservation Biology* 1(2): 150-153.
- TYLER, M.J. 1968. Papuan hylid frogs of the genus *Hyla*. *Zoologische Verhandlungen* 96: 1-203.
1982. The hylid frog genus *Litoria* Tschudi: an overview. *Proceedings of the New Zealand Herpetological Symposium, Occasional Publication* 2: 103-112.
1992. *Encyclopedia of Australian animals. Frogs*. (Angus & Robertson: Sydney).
- TYLER, M.J. & DAVIES, M. 1978. Species-groups within the Australopapuan hylid frog genus *Litoria* Tschudi (Anura: Hylidae). *Australian Journal of Zoology, Supplementary Series* 63: 1-47.
1979. Redefinition and evolutionary origin of the Australopapuan hylid frog genus *Nyctimystes* Stejneger. *Australian Journal of Zoology* 27(5): 755-772.
- TYLER, M.J., DAVIES, M. & APLIN, K. 1986. A new stream-dwelling species of *Litoria* (Anura: Hylidae) from New Guinea. *Transactions of the Royal Society of South Australia* 110(2): 63-67.
- WILLIAMS, S. & HERO, J.-M. 1998. Rainforest frogs of the Australian Wet Tropics: guild classification and the ecological similarity of declining species. *Proceedings of the Royal Society. London, B. Biological Sciences* 265: 597-602.

APPENDIX

SPECIMENS EXAMINED.

Litoria nannotis - All QM specimens of this species between registration numbers J17017 to J71334. Sample sizes: ♂ 60; ♀ 44; Juveniles: 22.

Litoria lorica - ♂ ♂: J36090 (holotype), J36092-93 (QM paratypes), R17349-50 (SAM paratypes), J42235 (QM new record), UMMZ202427-39; ♀ ♀: J36091 (QM paratype), R17351 (SAM paratype).

Litoria nyakalensis - ♂ ♂: J22624 (holotype), J22625-30 (paratypes), J29287, J32117, J34415, J43680, J43682-83, J43856, J52942, J54188, J55584, J55598, J55768; ♀ ♀: J55592, J55595-96, J55770, J55776-77, J55786.

Litoria rheocola - ♂ ♂: J22631 (holotype), J22632-42 (paratypes); ♀ ♀: J22643-45 (paratypes).

Nyctimystes dayi - ♂ ♂: J61844, J66044, J66127-28; ♀: J66108.

Litoria genimaculata - ♂ ♂: J43650, J43653, J53685, J53688, J53707, J53743 (cleared & stained), J56093; ♀ ♀: J53741, J53747 (cleared & stained), J56092.

Litoria pearsoniana - ♂ ♂: J70861, J70894, J72661; ♀: J68178.

Litoria lesueuri - ♂ ♂: J35611, J35620-21; ♀: J36068.

MORPHOLOGY AND DISTRIBUTION OF *AUSTRALOBIUS SCABRIOR* (CHILPODA: LITHOBIOMORPHA: LITHOBIIDAE)

GREGORY D. EDGECOMBE AND LAUREN M. HOLLINGTON

Edgecombe, G.D. & Hollington, L.M. 2002 5 31: Morphology and distribution of *Australobius scabrior* (Chilopoda: Lithobiomorpha: Lithobiidae). *Memoirs of the Queensland Museum* 48(1): 103-118. Brisbane. ISSN 0079-8835.

Australobius scabrior Chamberlin, 1920, is the type species of the Indo-Malay lithobiid genus *Australobius* Chamberlin, 1920, and was hitherto known from three specimens from the Wet Tropics, north Queensland. We revise the species based on extensive collections ranging from Cape York to Sydney, with one record in central Victoria. Electron microscopic study of *A. scabrior* permits documentation of morphological features not treated in previous work on the genus. *Australobius* is the only member of Lithobiidae native to Australia. □ *Australobius*, Chilopoda, Lithobiidae, Queensland, New South Wales.

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Australobius Chamberlin, 1920 is a widely distributed chilopod genus in the Indo-Malay region (Eason, 1978). Some 30 nominal species belong to the genus, which ranges from the Seychelles, Kazakhstan, Kirghizia and Nepal through southeast Asia and the Indonesian Archipelago to New Guinea and eastern Australia (Eason, 1980, 1986, 1989, 1992, 1993, 1997). The type species, *A. scabrior* Chamberlin, 1920, is the only recorded Australian species. Chamberlin (1920) described *A. scabrior* from a single specimen from Kuranda in north QLD. Eason (1974) cautioned that *A. scabrior* may be an introduced species, as no endemic Lithobiidae are otherwise known from Australia. Later, Eason (1996) announced the rediscovery of *Australobius scabrior* based on two specimens from Fitzroy Island on the Great Barrier Reef.

Previous work would thus indicate that native Lithobiidae are of uncertain status in Australia; Lithobiomorpha is otherwise represented by the Henicopidae, which has a predominantly southern temperate distribution. However, collections from many sites along the Great Divide demonstrate that *Australobius* is widely distributed and abundant in QLD, and occurs in NSW as far south as Sydney. We document the morphology of *Australobius* by electron microscope study, presenting a detailed description of characters (e.g. mouthparts) hitherto neglected. Availability of a large sample over a wide geographic range permits appraisal of intraspecific variation.

Abbreviations cited in this work are as follow:

AM – Australian Museum, Sydney; ANIC – Australian National Insect Collection, Canberra; CAS – California Academy of Sciences, San Francisco; MCZ – Museum of Comparative Zoology, Harvard University, Cambridge; NMV – Museum Victoria, Melbourne; NSW – New South Wales; QLD – Queensland; QM – Queensland Museum, Brisbane; UQ – University of Queensland, Brisbane; VIC – Victoria. Abbreviations for collectors are as follow: DC – D. Cook; DKY – D.K. Yeates; GAM – G.A. Milledge; GBM – G.B. Monteith; GC – G. Cassis; GDE – G.D. Edgecombe; GT – G. Thompson; HJ – H. Janetzki; MRG – M.R. Gray. Other abbreviations: Ck – Creek; NP – National Park; Ra. – Range; Rd – Road; rf – rainforest; SF – State Forest.

For electron microscopy, specimens were air-dried and photographed on a Leo 435VP using a Robinson backscatter collector.

SYSTEMATICS

Australobius Chamberlin, 1920

For synonymy see Eason (1978).

TYPE SPECIES. *Australobius scabrior* Chamberlin, 1920: by original designation.

Australobius scabrior Chamberlin, 1920

Australobius scabrior Chamberlin, 1920: 76; Eason, 1996: 91; Edgecombe et al., 2002: figs 3B, 8A,F.

HOLOTYPE. MCZ. 14538 (TC-189), male, Kuranda, QLD, H.L. Clark, 6-8.ix.1914.

OTHER MATERIAL. Not all early post-larval stages [e.g., Agenitalis stage(s)] have been sexed, in which case they are recorded simply as juvenile.

NORTHEASTERN QUEENSLAND (CAPE YORK).
ANIC: female, 9km ENE Mt Tozer, 12°43'S 143°18'E, T. Weir, 11-16.vii.1986, rf; ♂, 2 juveniles, larva, 3km ENE Mt Tozer, 12°44'S 143°14'E, T. Weir, 14.vii.1986; ♀, McIlwraith Ra., 13°45'S 143°20'E, c. 400m, R.W. Taylor, 27.vii.1977, rf; 5 ♀♀, 4♂♂, 9 juveniles, 6 larvae, McIlwraith Ra., 11km W by N Bald Hill, 13°44'S 143°20'E, 520m, T.A. Weir, 27.vi.-12.vii.1989; UQ: ♀, Lankelly Ck, McIlwraith Ra., near Coen, B. Cantrell, 28-31.x.1969.

NORTHEASTERN QUEENSLAND (WET TROPICS).
QMS18010, 2♂♂, Mossman Bluff, 10km W Mossman, 16°26'54"S 145°16'53"E, 1100-1300m, GBM and GT, 17-18.xii.1988; QMS21803, ♂, Mt Lewis Rd, 10km N Mt Lewis, 16°31'17"S 145°16'23"E, 1100m, GBM, GT, DC, Sheridan and HJ, 25.xi.1990; QMS45074, ♂, 2 juveniles, QMS45075, ♂, 2.5km SW Mt Hartley, 15°47'S 145°19'E, 610m, GBM, DKY and DC, 24.iv.1982, rf; QMS45076, male, Mt Finnigan, summit, 15°48'S 145°17'E, 1100m, GBM and DC, 30.xi.1985, rf; QMS45077, ♂, Mt Finnigan via Helenvale, 15°48'53"S 145°16'28"E, 850-950m, GBM, GT, DC, Sheridan and Roberts, 3-5.xii.1990; QMS45078, ♂, Mt Finley, 15°49'S 145°21'E, Qld. Mus., 2.xii.1975; QMS45079, ♀, ♂, 12 Mile Scrub, RM and V.E. Davies, 22-27.xi.1975; QMS45080, 4 ♀, 6 ♂, Mt Halcyon, 16°03'S 145°25'E, 870m, GBM and HJ, 24.xi.1983, rf; QMS45081, ♂, QMS45082, ♂, Mt Pieter Botte, 16°04'S 145°24'E, 950m, GBM, HJ, Roberts and DC, 21.xi.-8.xii.1993; QMS45083, 2 ♂, Roaring Meg Ck, 6km W Cape Tribulation, 16°04'S 145°24'E, 740m, GBM, DKY and GT, 5.x.1982, rf; QMS45084, ♀, Pilgrim Sands, 16°04'20"S 145°28'E, R.J. and S. Raven and P. and E. Lawless, 29.xi.1992-17.iv.1993; QMS45085, ♂, 4.5-5km W Cape Tribulation (Top Camp), 16°05'S 145°26'E, 760-780m, GBM, DKY and GT, 2.x.1982, rf; QMS45086, ♀, QMS45087, ♂, QMS45088, ♂, 1.5km NW Cape Tribulation, 16°05'S 145°28'E, 0m, GBM, DKY and GT, 3.x.1982-23.iv.1983, rf; QMS45089, ♂, QMS45090, ♂, juvenile, 2km WNW Cape Tribulation, 16°05'S 145°28'E, 50m, GBM, i.1983, GBM, DKY and GT, 3.x.1982 rf; QMS45091, 2 larvae, QMS45092, 2 ♂, 1.5km W Cape Tribulation, 16°05'S 145°28'E, 150m, GBM and DKY, 2.i., 21.iv.1983, rf; QMS45093, ♀, 3 ♂, larva, QMS45094, ♀, 2.5km W Cape Tribulation, 16°05'S 145°27'E, 180m, GBM and DKY, 2.i., 20-23.iv.1983, rf; QMS45095, ♀, QMS45096, ♀, ♂, 2 larvae, 2.7km W Cape Tribulation, 16°05'S 145°27'E, 400m, GBM, i.1983, rf; QMS45097, ♂, QMS45098, larva, 4.5km W Cape Tribulation, 16°05'S 145°26'E, 760m, GBM and DKY, i.1983, 23.iv.1983, rf; QMS45099, ♀, 5km W Cape Tribulation, 16°05'S 145°26'E, 780m, GBM, DKY and GT, 29-30.ix.1982, rf; QMS45100, 7 ♀, 6 ♂, Mt Hemmant, 16°07'S 145°25'E, 1050m, GBM and HJ, 27.xi.1993, rf; QMS45107, 3 ♀, Table Mt, 10km S Cape Tribulation, 16°09'S 145°26'E, 320m, GBM and DC, 24.iv.1983, rf; QMS45108, ♂, Thornton Peak via Daintree, 1000-1300m, GBM and DC, 20-22.xi.1981; QMS45109,

♂, QMS45110, ♀, ♂, Thornton Peak, 11km NE Daintree, 16°10'S 145°22'E, 1100-1200m, GBM, DKY and GT, 30.x.-1.xi.1983; QMS45111, ♂, QMS45112, ♀, Thornton Peak, 1100-1300m, GBM and S.R. Monteith, 24-27.ix.1984; QMS45113, ♂, Devil's Thumb, 12km NW Mossman, 1000m, ANZSES, 27.xii.1989; QMS45114, 2 ♀, ♂, Mt Spurgeon via Mt Carbine, 16°27'S 145°12'E, 1100m, GBM and GT, rf; QMS45115, ♂, 4 juveniles, QMS45116, ♀, ♂, QMS45117, ♀, The Bluff, 11km W Mossman, 16°27'S 145°16'E, 1050m, GBM and DKY, 27.iv.1983, rf; QMS45118, ♂, The Bluff, 1100m, GBM, DKY and GT, 2.xi.1983; QMS45119, ♀, Spear Ck, V.E. Davies and R. Raven, 3-10.xi.1975; QMS45120, ♀, ♂, QMS45122, ♂, QMS45123, ♂, Windsor Tableland, 35km NNW Mt Carbine, 1050m, 850m, GBM, DKY and DC, 16-26.iv.1982, rf; QMS45124, ♂, Mossman Bluff track, 9-10km W Mossman, GBM and GT, ANZSES, 21.xii.1989; QMS45125, ♂, QMS45126, 2 ♂, Mt Demi, 7km SW Mossman, 16°30'S 145°19'E, 900-1000m, GBM and DKY, 26.iv.1983, rf; QMS45127, ♀, 5.5km N Mt Lewis via Julatten, GBM and DC, 1100m, rf; QMS45128, 2 ♀, 2 ♂, Mt Lewis, Upper Leichhardt, 16°35'S 145°16'E, 840m, GBM, 18.xi.1997, rf; QMS45129, ♀, Kingfisher, Julatten, 16°36'S 145°21'E, 400m, GBM, 18.xi.1997, rf; QMS45130, ♀, Mt Gorton, 16°57'S 145°53'E, 750m, HJ, 18.xi.1993, rf; QMS45131, ♂, Copperlode Dam Rd, 16°58'30"S 145°42'30"E, P. Lawless, R. Raven and M. Shaw, 27.x.1991-23.vii.1992; QMS45132, ♂, QMS45133, ♀, Lambs Head, 10km W Edmonton, 17°01'23"S 145°38'33"E, 1200m, GBM, GT and HJ, 10-12.xii.1989; QMS45133, ♀, Lamb's Head, 10km W Edmonton, 1200m, GBM, GT and HJ, 10-12.xii.1989; QMS45134, 4 ♀, 3 juveniles, Lamb's Head, 20km SW Cairns, 17°02'S 145°39'E, 1200m, GBM, 10.xi.1981, rf with *Agathis*; QMS45135, 4 ♀, 5 ♂, Mt Murray Prior, 16°56'S 145°51'E, 770m, GBM, 30.x.1995, rf; QMS45136, 2 ♂, 2 juveniles, North Bell Peak, via Gordonvale, 900-1000m, GBM and DC, 16.ix.1981, rf; QMS45137, ♂, Bell Peak North, 10km E Gordonvale, 17°06'S 145°53'E, 850-1000m, GBM, DKY and GT, 13.x.1982, rf; QMS45138, ♂, Cathedral Fig, 13km NW Yungaburra, 17°11'S 145°39'E, 750m, GBM and GT, 10.xii.1988, rf; QMS45139, ♀, Massey Ra., 12km S Gordonvale, 17°16'S 145°49'E, 1300m, GBM, 2.v.1983, rf; QMS45140, 2 ♀, 5 ♂, Russell River at Bellenden Ker Landing, 17°16'S 145°49'E, 5m, Earthwatch/Qld. Mus., 24-31.x.1981; QMS45146, larva, same locality, palm swamp, moss on tree trunks; QMS45141, 3 ♀, 3 ♂, 4 juveniles, 3 larvae, QMS45142, 8 larvae, QMS45143, 4 ♀, 4 ♂, 5 juveniles, six larvae, Bellenden Ker Ra., Cableway Base Stn, 17°16'S 145°54'E, 100m, Earthwatch/Qld. Mus., 17-24.x.1981, rf; QMS45145, ♀, 4 ♂, 5 juveniles, larva, same locality, 25-31.x.1981; QMS45147, juvenile, QMS45148, ♂, QMS45149, juvenile, QMS45150, 2 ♀, ♂, larva, Bellenden Ker Ra., Cable Tower 3, 17°16'S 145°52'E, 1054m, Earthwatch/Qld. Mus., 25-31.x.1981, rf; QMS45151, ♀, 2♂, Bellenden Ker Ra., Cable Tower 5, 532m, Earthwatch/Qld. Mus., 17-24.x.1981; QMS45152, ♂, Bellenden Ker Ra., 1km S Cable Tower 6, 500m, Earthwatch/Qld. Mus., 17.x.-5.xi.1981; QMS45153, ♀, Bellenden Ker Ra.,

- 0.5km S Cable Tower 7, 500m, Earthwatch/Old. Mus., 25-31.x.1981; QMS45154, ♀, 2 ♂, QMS45155, female, QMS45156, ♂, QMS45157, ♂, QMS45158, ♂, Bellenden Ker Ra., Summit TV Stn, 17°16'S 145°51'E, 1560m, Earthwatch/Old. Mus., 17.x.-7.xi.1981, rf; QMS45159, ♀, ♂, QMS45160, male, Bellenden Ker Ra., summit TV Stn, 17°16'S 145°51'E, 1560m, GBM and DKY, 29.iv.-2.v.1983, rf; QMS45161, ♂, 3 juveniles, Mt Bartle-Frere, summit creek, 1500m, GBM and DC, 24.ix.1981, rf; QMS45162, ♀, Mt Bartle-Frere, W. base, 17°23'S 145°46'E, 1230m, GBM and Hasenpusch, 7.iii.-15.v.1995; QMS45163, 4 ♂, QMS45164, 2 ♂, Mt Bartle-Frere, 0.5km N of Sih peak, 17°24'S 145°49'E, 1500m, QMS45168, ♀, ♂, 2 juveniles, Sih Peak summit, 1620m, Earthwatch/Old. Mus., 6-8.xi.1981, rf; QMS45165, ♂, Mt Bartle Frere, Central Ridge, 1500m, GBM, 27.xii.1989; QMS45166, juvenile, S.45167, female, Mt Bartle-Frere, NW/Centre Peak ridge, 17°23'S 145°48'E, 1400-1500m, Earthwatch/Old. Mus., 7-8.xi.1981, rf; QMS45169, ♂, Boonjee, R. Raven and V.E. Davies, 3-6.iv.1978; QMS45170, ♂, Hughes Rd, Topaz district, 17°26'S 145°42'E, 650m, GBM and HJ, 5.xii.1993, rf; QMS45171, ♀, QMS45172, 3 ♀, 2 ♂, tower S of Crater NP, 17°27'S 145°29'E, 1230m, GBM and J. Hasenpusch, 25.xi.1994-10.i.1995 (S. 45171), GBM, 16.v.1995 (S. 45172), rf; QMS45173, ♂, Stone Ck, 17°28'S 146°01'E, 100m, J. Hasenpusch, 1.xi.1995-6.ii.1996; QMS45174, 3 ♀, 2 ♂, Mt Fisher (Kjellberg), 17°32'S 145°33'E, 1100m, GBM, 17.v.1995, rf; QMS45175, ♀, Mt Father Clancy, 9km S. Millaa Millaa, 950m, GBM and GT, 6.xii.1988; QMS45176, ♂, Upper Boulder Ck, 11km NNW Tully, 1000m, Davies, GBM, Gallon, DC and GT, 17-18.xi.1984; QMS45177, 2 ♂, Mt Pershouse, Kirrama Ra., 18°12'S 145°45'E, 930m, GBM and GT, 12.xii.1986, rf; QMS45178, 2 ♂, Cardwell Ra., Upper Broadwater Ck Valley, 750m, GBM, GT and S. Hamlet, 18.xii.1986-14.i.1987, rf; QMS45195, ♀, Gap Ck, 12 Mile Scrub, V.E. Davies, 23-28.xi.1975; AM KS 57831, ♂, Goldsborough Valley SF, ca. 1.5km from campsite, 17°14'S 145°46'E, GAM and H. Smith, 22.v.2000, rf; AM KS 57859, ♀, Goldsborough Valley SF, ca. 15km from Atherton Rd, 17°13'35"S 145°45'49"E, GAM and H. Smith, 22.v.2000, rf; AM KS 57863, ♂, Cardwell Ra., Kirrama Rd, 4.5km from turnoff from Kennedy Ck Rd, 18°11'54"S 145°51'59"E, GAM and H. Smith, 24.v.2000; AM KS68715, ♀, ♂, Mount Lewis, 11.3km from rd between Mossman and Mount Molloy, 16°35'31"S 145°16'15"E, 1000m, GDE and GAM, 30.iv.1998, rf; AM KS68716, ♀, Tully Gorge NP, Tully Gorge lookout, 17°46'37"S 145°33'23"E, 700m, GAM, 23.iv.1998; AM KS68717, ♀, Clohesy River SF, 3.3km SE Kennedy Highway, 16°55'20"S 145°36'14"E, GDE and GC, 5.v.1998, wet sclerophyll; AM KS68718, Mount Hypipamee NP, 17°25'29"S 145°29'00"E, GDE, GC and GAM, 25.iv.1998, rf; AM KS68719, 2 ♂, Tinaroo Dam area, Robson Ck Rd, 17°06'12"S 145°37'40"E, GDE, GC and GAM, 26.iv.1998, rf; ANIC, 14 ♀, 4 ♂, Mt Webb NP, 15°04'S 145°07'E, A. Calder and J. Feehan, 27-30.iv.1981; ANIC, 6 ♀, 4 ♂, 1.5km E by N Mt Sorrow, 16°05'S 145°27', A. Calder and T. Weir, 25.iii.1984, rf; ANIC, ♂, Noah Ck, 7km ENE Thornton Peak, 16°08'S 145°26'E, A. Calder and T. Weir, 27.iii.1984, rf; ANIC, 2 ♀, Mt Lewis, 16°33'S 145°13'E, 970m, R.W. Taylor, 8.ix.1975; ANIC, ♀, 38km W Kuranda, 16°45'S 145°25'E, J.G. Brooks, 12.ii.1970, rf; ANIC, 4 ♀, 2 ♂, Kuranda, 16°45'S 145°35'E, 430m, R.W. Taylor, 29.vii.1977, rf; ANIC, ♂, Eacham NP, 17°18'S 145°37'E, J.G. Brooks, 11.i.1971; ANIC, ♂, Mt Fisher, 17°33'S 145°32'E, 1150m, P. Zborowski, 5.iv.-3.v.1995; ANIC, 6 ♀, 5 ♂, Crawford Lookout, 17°37'S 145°48'E, R.W. Taylor and J. Feehan, 5.vii.1971; ANIC, ♀, McNamee Ck, 17°40'S 145°49'E, ca 300m, R.W. Taylor and J. Feehan, 8.vii.1971, rf; CAS, ♂, 1mi. NE Ravenshoe, 975m, E.S. Ross and D.Q. Cavagnaro, 7.xi.1962; CAS, ♂, Malanda, 700m, E.S. Ross and D.Q. Cavagnaro, 8.xi.1962; CAS, ♂, The Boulders, near Babinda, 100m, E.S. Ross and D.Q. Cavagnaro, 10.xi.1962; CAS, 2 ♀, ♂, Cape Tribulation NP, Emmagen Ck, 16°04'S 145°27'E, sea level, C.E. Griswold, 26.vii.1992, rf.
- MID-EASTERN QUEENSLAND. QMS45179, ♀, S.45180, 2 ♀, ♂, Mt Dryander summit, 20°15'S 148°33'E, 740m, GBM, 24.iv.1979, rf; QMS45181, QMS45182, 2 ♂, Conway SF, Brandy Ck Rd, 20°20'S 148°42'E, 60m, GBM, 23, 25.iv.1979, rf; QMS45183, ♀, Cathu SF, Mt Macartney, 20°51'S 148°33'E, 750m, GBM, 22.iv.1979, rf; QMS45185, ♀, Eungella NP, Broken River, 21°10'S 148°30'30"E, R. Raven, P. and E. Lawless and M. Shaw, 29.vii.-4.xii.1992; AM KS68720, 3 ♂, Eungella NP, Dalrymple Rd, 1.7km NE Snake Rd, 21°04'S 148°34'30"E, GDE, S. Davis and GAM, 18 and 21.iv.1998, rf; ANIC, ♀, Finch Hatton Gorge, 21°05'S 148°38'E, 200m, R.W. Taylor and A. Weir, 11.xi.1976, rf; ANIC, ♀, 3 ♂, Eungella NP, 21°09'S 148°30'E, 760m, R.W. Taylor and A. Weir, 10.xi.1976, rf; CAS, ♀, 2mi. E Eungella, 450m, E.S. Ross and D.Q. Cavagnaro, 18.xi.1962; CAS, ♀, 8mi. NE Eungella, 950m, E.S. Ross and D.Q. Cavagnaro, 18.xi.1962.
- SOUTHEASTERN QUEENSLAND. QMS45186, ♀, Kroombit Tops, 24°22'S 150°59'E, R. Raven, 25.xi.1982; QMS45187, ♂, ♀, Marys Ck SF via Gympie, 26°15'44"S 152°33'40"E, 183m, GBM and S.R. Monteith, 1974-1975; QMS45188, ♂, Cooloola, E.C. Dahms, 21.viii.1970, rf; QMS45189, ♀, ♂, Cooloola, 25°57'31"S 153°06'54"E, V. E. Davies and R. Raven, 4.ii.1976; QMS45190, ♀, ♂, Mary Cairncross Park, via Maleny, 26°46'52"S 152°52'56"E, 488m, GBM and S.R. Monteith, 1974-1975; QMS45191, ♂, Brookfield, 27°29'46"S 152°54'25"E, 110m, GBM and S.R. Monteith, 1974-1975; AM KS68721, intersection of Sunday Ck Rd and Gigher Ck Rd, 26°41'54"S 152°33'05"E, GDE, S. Davis and GAM, 7.v.1998, wet sclerophyll; AM KS68722, ♀, ♂, Kenilworth SF, Sunday Ck Rd, 9.8km W of Charlie Moreland Park, 26°40'11"S 152°36'35"E, GAM, 6 and 7.v.1998, wet sclerophyll; AM KS68723, ♀, Kenilworth SF, Booloumba Ck Rd, 26°41'13"S 152°37'06"E, GAM, 6.v.1998, wet sclerophyll.
- NEW SOUTH WALES. AM KS68724, ♂, Border Ranges NP, 450m N Sheep Station Ck camping area, 28°24'S 153°01'E, MRG and GC, 4.ii.-9.iv.1993; AM KS51014, ♂, Tweed Ra., 28°26'S 152°53'E, 300-400m, Smith,

Hines, Pugh and Webber, 22.ii.1989, rf; AM KS68725, 2 ♂, Richmond Ra. SF, Goanna Ck Rd, 0.4km from junction with Sandy Ck Rd, 28°37'S 152°42'E, 575m, MRG and GC, 4.ii.-9.iv.1993; AM KS68726, ♂, Whian Whian SF, Big Scrub Flora Reserve, Gibbergunyah Ra. Rd, 150m W Rocky Ck crossing, 28°38'S 153°19'E, 180m, MRG and GC, 4.ii.-9.iv.1993; AM KS68727, ♀, 5.9km NE from creek crossing on Morgan Ck, 28°46'S 152°18'E, 620m, MRG and GC, 4.ii.-9.iv.1993; AM KS9356, ♀, Washpool NP, Coombadjah Ck, 29°16'S 152°22'E, C. Horseman, 12.ii.1982; AM KS68728, ♂, Chaelundi SF, 3.8km W along Stockyard Fire Trail from Chandler Ck, 29°57'S 152°32'E, 450m, MRG and GC, 4.ii.-9.iv.1993; AM KS68729, ♀, Marengo SF, 0.4km SW along Chimney Rd from junction of Buckboard and Foamy Ck Rds, 30°06'S 152°25'E, 1090m, MRG and GC, 4.ii.-9.iv.1993; AM KS68730, ♀, Dorriggo NP, Dome Rd, about 1km W Never Never picnic area, 30°21'S 152°47'E, 690m, MRG and GC, 4.ii.-9.iv.1993; AM KS68731, ♀, Enfield SF, Dodds Fire Trail, about 3km from Enfield Rd, 31°24'S 151°52'E, 910m, MRG and GC, 4.ii.-9.iv.1993; AM KS68732, ♀, Bulga SF, Wild Cattle Ck, 400m NE Spur Track, 31°36'S 152°07'E, 400m, MRG and GC, 4.ii.-9.iv.1993; AM KS68733, ♀, Wilson River Flora Reserve, 31°12'S 152°28'E, 244m, GDE and Z. Johanson, 3.xii.1999, rf; AM KS35583, ♂, Lorient Wildlife Refuge, 3km N Lansdowne via Taree, G. Williams, 14.viii.1990; AM KS35859, 2 ♀, ♂, Kiwarak SF, S Taree, G. Williams, 25.ii.1991; AM KS68734, ♀, Chichester SF, Barrington Tops, Middle Ridge Rd, 550m N Dixies Top trail, 32°10'S 151°42'E, GDE and Z. Johanson, 15.iii.1999; AM KS68735, ♀, Allyn Stn, Barrington Tops, P.M. Johns, 19.i.1975, rf; AM KS 58467, ♂, Woodford, Ridge St, 33°43'50"S 150°28'40"E, Aust. Mus. Bus. Serv., 30.ix.1996; AM KS44882, ♀, Jamieson Park, Narrabeen, 33°43'S 151°18'E, 20m, MRG and H.M. Smith, 6-20.xi.1995, *Angophora costata* woodland; AM KS 72034, ♂, Sydney Harbour NP, Bradleys Head, GDE, 14.vii.2001; QMS45192, ♀, Whian Whian SF, via Dunoon, 28°38'25"S 153°20'01"E, 200m, GBM and S.R. Monteith, 1974-1975; QMS45193, ♂, Victoria Park, via Alstonville, 28°54'20"S 153°24'37"E, 213m, GBM and S.R. Monteith, 1974-1975; QMS45194, ♀, Brunxner Park, via Coffs Harbour, 30°15'00"S 153°06'10"E, 150m, GBM, 1980-1981, rf; CAS, ♀, 2 ♂, near Catherine Hill Bay, 60m, E.S. Ross and D.Q. Cavagnaro, 2.xii.1962.

VICTORIA. NMV61, ♀, Fraser NP, A. Burns, 29.xi.1946.

ECOLOGY. Most specimens were collected in rainforest, though in SE QLD (Fig. 1) *A. scabrior* appears to be more common in wet sclerophyll forest than in the adjacent rainforest. The species is collected in greatest abundance under the bark of standing eucalypts, with as many as 20 specimens obtained from a single large tree (AM KS 68721). The total altitudinal range is from near sea level to 1560m. The species has been collected year-round; in NE QLD, records are concentrated in October-December and March-May.

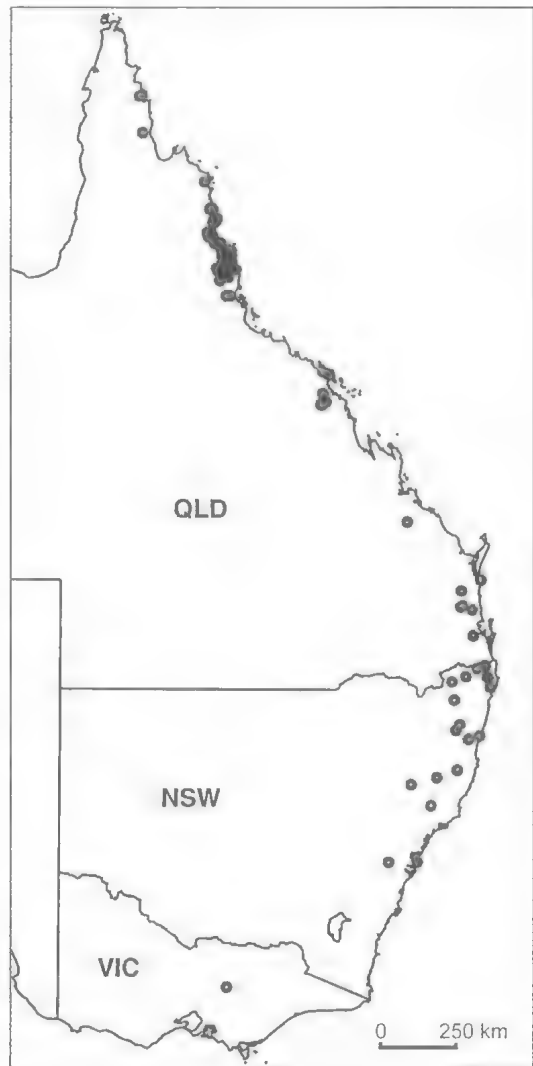


FIG. 1. Distribution of *Australobius scabrior* in eastern Australia.

DESCRIPTION. Maximum length (head shield to end of telson) 17.1mm (QMS45116, Fig. 2); maximum width of head shield 2.4mm; antenna 8.7mm long; anal leg 6.6mm long from trochanter to pretarsus.

Colour. Head and tergites mottled reddish brown, occasionally with slight purple tinge. Antenna light orange-brown, brighter orange distally. Maxillipede coxosternite and telopodite pale orange. Trunk sternites generally pale yellow with light purple tinge; sternites 14-15, genital sternite and gonopods pale orange. Legs

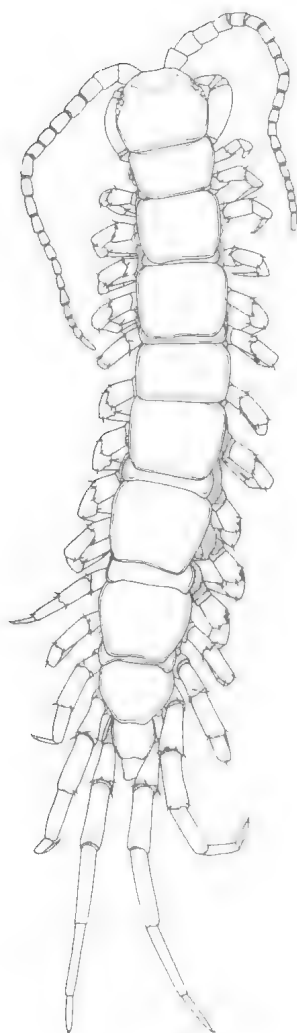


FIG. 2. *Australobius scabrior* Chamberlin, 1920. Dorsal view of male, QMS45116, The Bluff, 11km W Mossman, Qld. Width of head 2.4mm.

pale proximally, purple pigmentation increasing to tibia; tarsus pale orange; 14th and 15th legs commonly striped with alternating purplish-brown and white bands, podomeres less pigmented distally.

Head shield. Head as broad as long, or slightly broader, feebly concave posteriorly; head smooth relative to tergites, wider than TT1-5, about equal in width to T7; marginal ridge running along posterior margin and halfway along each side; ridge thickened posteromedially (Fig. 3A). Anterior third of head shield bounded posteriorly with transverse suture; antennocellar suture with

anterior branch running forwards and inwards to base of antenna, posterior branch running to marginal notch, behind major ocellus. Longitudinal median furrow on anterior part of head shield incised for about $\frac{3}{4}$ length to transverse suture. Posteromedian depression shallow.

Clypeus with blunt, triangular projection bearing a number of large setae on its apex (Fig. 4A); lateral margins of this projection fringed by shorter setae. Posterior margin of clypeus concave; row of four short setae medially, directly in front of labrum (Fig. 4B). Labral sidepiece fringed posteriorly with bristles (Fig. 4B) which are branched extensively (Fig. 4C). Labral midpiece bears small rectangular tooth with small notch on each side; another pair of larger, rounded notches separate sidepiece from midpiece on each side (Fig. 4B); slender transverse seta extends from a depression anterior to each of these notches, extending to rectangular tooth.

Antenna. Antenna consistently slightly less than half length of body. 17-23 articles, overwhelming majority of specimens with 20 articles on each side; articles slightly elongate, covered with long straight setae (finely ridged trichoid sensilla) on all sides (Fig. 3B,D); two widely separated, digitiform thin-walled basiconic sensilla on anterior face of each article along its anterior sclerotised edge, just behind band of arthrodial membrane that separates articles. Terminal article typically 2.5 times as long as broad, 1.4-2.1 times length of preceding article.

Ocelli. Pale. Major ocellus circular or narrowly elliptical, usually slightly larger than largest of seriate ocelli, sometimes equal in size; five or six (exceptionally seven) seriate ocelli in two rows (Fig. 5); usually three ocelli in superior row, at least two, often three, in inferior row; ocelli of inferior row frequently slightly smaller than those of superior row; seriate ocelli usually contiguous. Major ocellus less raised than seriate ocelli, distinguished from surrounding area by lack of pores and setae (Fig. 3G); surfaces of lenses bear fingerprint-like ridges (Fig. 3H). Tömösváry organ situated on subtriangular sclerotisation immediately below and usually between the anterior two ocelli of inferior row (Fig. 3C,E). Tömösváry organ slightly elliptical, much smaller than all ocelli, surrounded by raised rim; sclerotisation bearing Tömösváry organ bordered anteriorly and posteriorly by arthrodial membrane with warty texture (Fig. 3F).

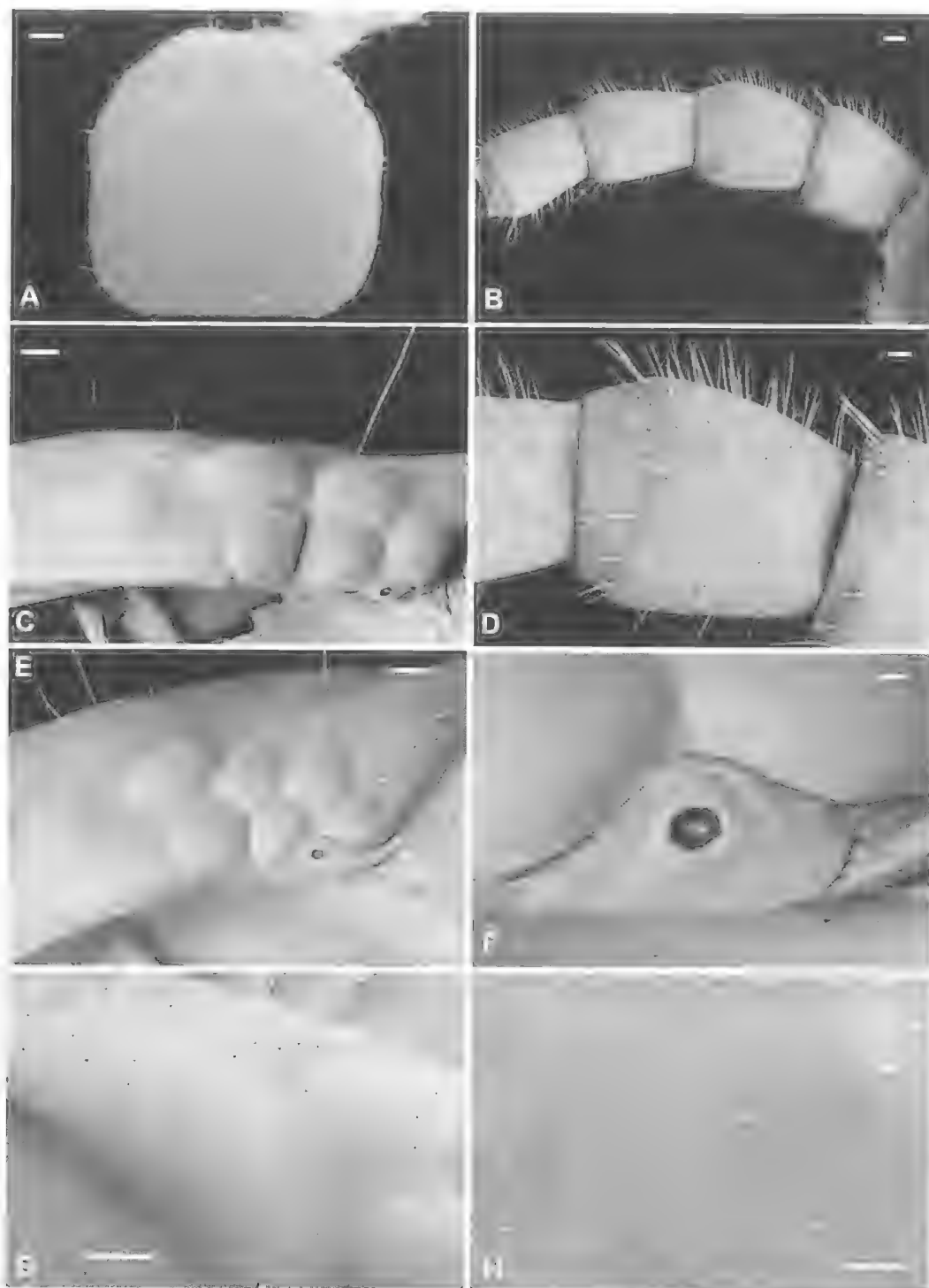


FIG. 3. *Australobius scabrior* Chamberlin, 1920. SEMs. A, AM KS68721, female, Kenilworth SF, SE Qld. Dorsal view of head shield, scale 200 μ m. B, D-H, AM KS9356, female, Washpool NP, NSW. B, D, proximal part of antenna, ventral views, scales 100 μ m, 50 μ m; E, ocelli, scale 50 μ m; F, Tömösváry organ, scale 10 μ m; G, H, major ocellus and surface of lens, scales 50 μ m, 3 μ m. C, AM KS68718, female, Mt Hypipamee NP, NE Qld. Ocelli, scale 50 μ m.

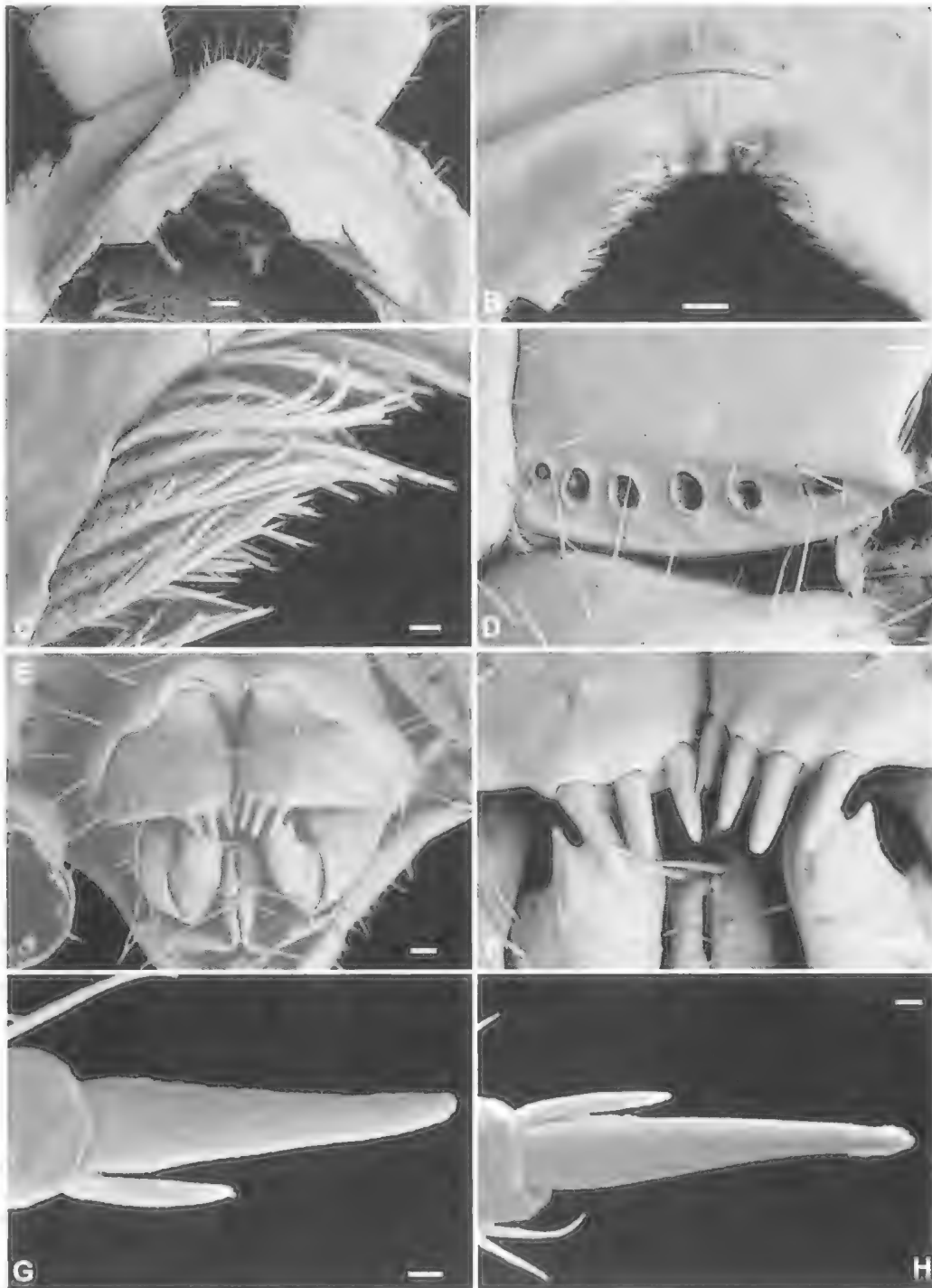


FIG. 4. *Australobius scabrior* Chamberlin, 1920. SEMs. A-F, AM KS9356, female, Washpool NP, NSW. A, ventral view of clypeus and labrum, scale 100µm; B, labrum, scale 50µm; C, bristles on labral margin, scale 5µm; D, coxal pores on leg 15, scale 50µm; E, gonopods, scale 50µm; F, spurs and claws on gonopods, scale 50µm. G-H, AM KS68721, female, Kenilworth SF, SE Qld. G, pretarsus of leg 14, scale 10µm; H, pretarsus of leg 15, scale 10µm.

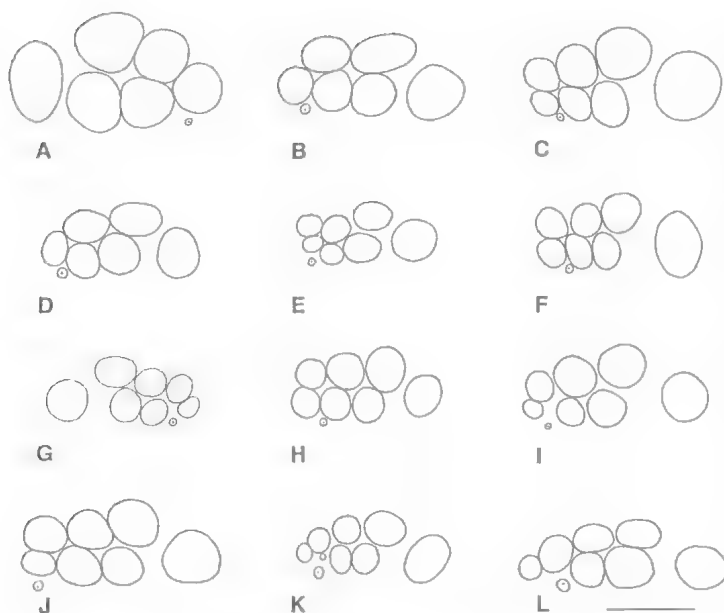


FIG. 5. *Australobius scabrior* Chamberlin, 1920. Arrangements of ocelli and Tömösváry organ. A-C, NE QLD; D-E, ME QLD; F-H, SE QLD; I-L, New South Wales. A, QMS45085, W Cape Tribulation; B, QMS45132, Lambs Head, W Edmonton; C, QMS45176, Upper Boulder Ck, NNW Tully; D, AM KS68720, Eungella NP; E, QMS45182, Conway SF; F, QMS45191, Brookfield; G, QMS45189, Cooloola; H, QMS45187, Marys Ck SF via Gympie; I, AM KS68724, Border Ranges NP; J, AM KS68729, Marengo SF; K, AM KS35583, Lorient Wildlife Refuge; L, AM KS44882, Narrabeen. Scale for all figures 0.25mm.

Maxillipede. Coxosternite roughly trapeziform, with feebly convex lateral margins (Fig. 6A, B, F). Dental margin set off as a rim by furrow that is impressed behind all but outermost teeth; rim extends backward from median notch, terminating at median suture (Fig. 6E); each half of dental margin convex (Fig. 7), separated by U-shaped median notch; teeth strongly chitinated; teeth closest to median notch largest, with outer teeth smaller (Fig. 6C,E,G); lateral teeth situated posteriorly in relation to other teeth (Fig. 6C); number of prosternal teeth in large specimens ranges from 4+4 to 10+9 (Fig. 11). Porodont small, about the size of large seta, arising from shallow, semi-circular socket, generally between second and third teeth as counted from medial to lateral (Fig. 6E,H). Coxosternite sparsely covered in setae, typically concentrated in anterior half (Figs 6B,F,7), abundant pores (Fig. 6C); surface of teeth ornamented with interconnected polygons, with an occasional pore between polygons (Fig. 6D). Telopodite bearing long, straight setae and many

pores on all segments (Fig. 6G); pretarsal and tarsal parts of tarsungulum about equal in length.

Mandible. Shank of mandible divided by single fissure separating lamina condylifera. Dentate lamella composed of four tricuspid teeth, single-cusped fifth tooth on one side (Fig. 8A, H); teeth bear rows of serrated accessory denticles (Fig. 8H); field of accessory denticles set off by strong grooved ridge. Furry pad a tuft of small, curved, faintly plumose bristles, strongly differentiated from accessory denticles on mandibular teeth. Pectinate lamella of approximately 10 large, sickle-shaped aciculae, strongly serrated on their concave edges (Fig. 8E-G); separate cluster of five larger aciculae extending from ventral margin of mandible (Fig. 8E); each acicula bears median ridge on internal surface, with pinnate margins (Fig. 8F). Inner ventral margin of mandible with row of three small, curved spines (Fig. 8D). Two narrow rows of small branching bristles fringe mandibular teeth (Fig. 8C),

extending from furry pad (Fig. 8H) to (approximately) ventral margin of third tooth, where the two rows grade into a single row of long plumose bristles that extends to ventrolateral margin of mandible (Fig. 8B, E); plumose bristles evenly branching along their length apart from hairless base (Fig. 8G).

First maxilla. Coxosternite divided medially, median suture terminates in front of tiny triangular sternite. Coxal projection conical, with large tuft of setae at apex (Fig. 9E); setae of three types: straight, finely ridged setae, found on all parts of projection (Fig. 9C); small plumose setae, generally found near lateral margin of projection (Fig. 9C), and compound setae, which superficially resemble simple setae, but are composed of numerous threadlike hairs extending together from a common base (Fig. 9D). Cluster of several sensilla microtrichoidea between coxal projection and telopod. Distal article of first maxillary telopod fringed medially with rows of large, densely plumose setae (Fig.

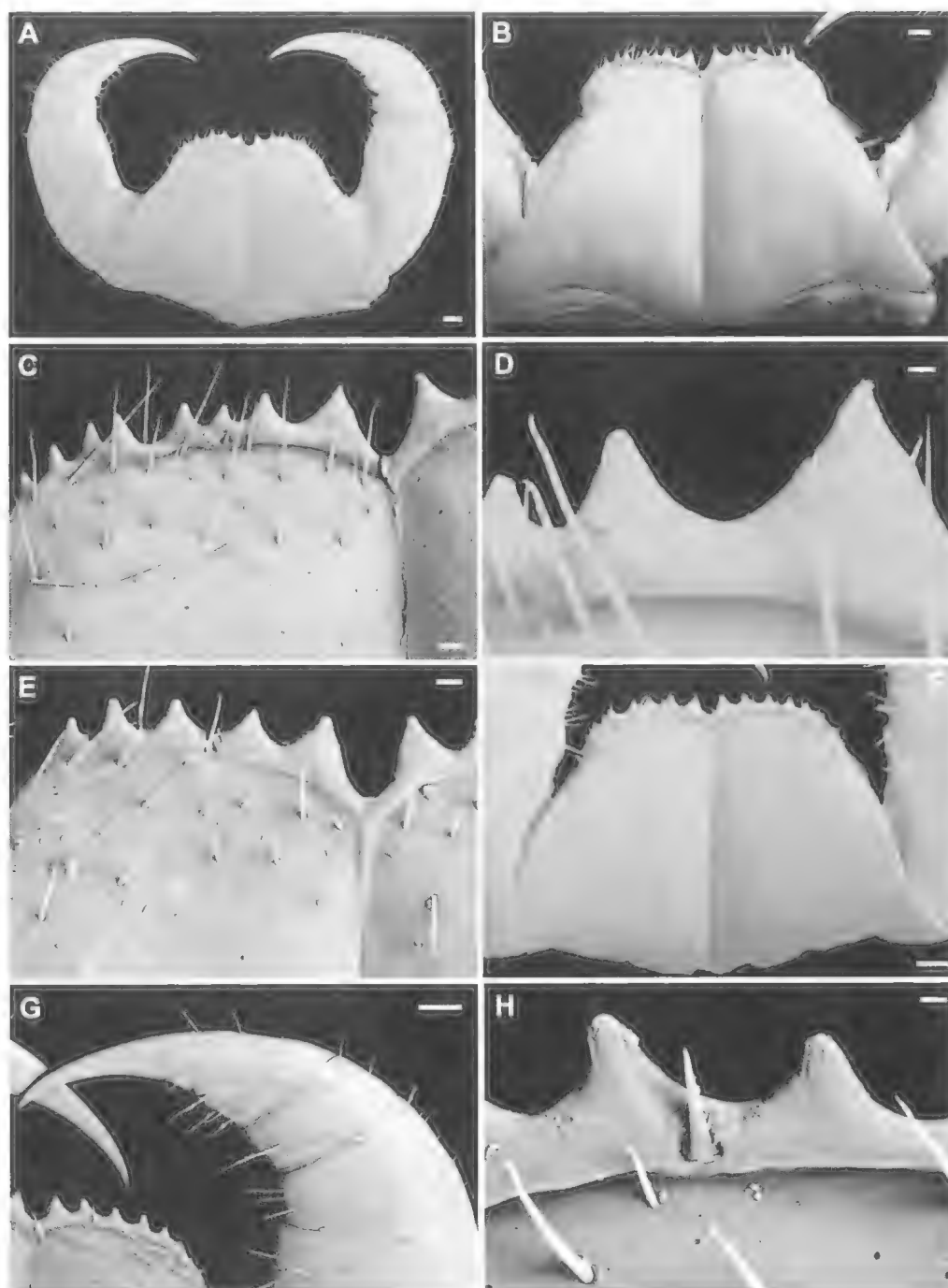


FIG. 6. *Australobius scabrior* Chamberlin, 1920. SEMs of maxillipede. A, AM KS68721, ♀, Kenilworth SF, SE Qld. Ventral view of maxillipede, scale 100µm. B-D, AM KS9356, female, Washpool NP, NSW. B, ventral view of coxosternite, scale 100µm; C, D, dental margin of coxosternite, detail of inner teeth (porodont at left), scales 30µm, 10µm. E, AM KS68718, female, Mt Hypipamee NP, NE Qld. Dental margin of coxosternite, scale 30µm. F-H, AM KS68725, ♂, Richmond Ra. SF, NSW. F, ventral view of coxosternite, scale 100µm; G, distal part of telopodite, scale 100µm; H, dental margin of coxosternite, showing porodont, scale 10µm.

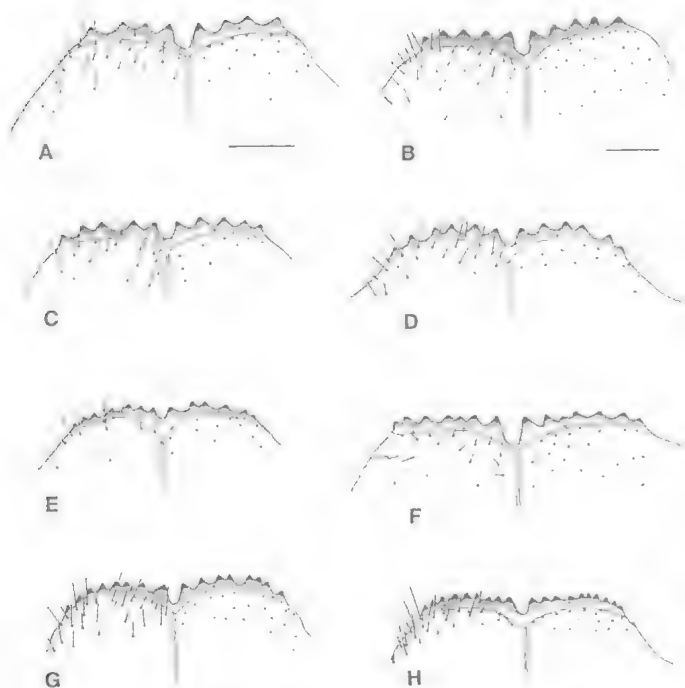


FIG. 7. *Australobius scabrior* Chamberlin, 1920. Maxillipede coxosternite, showing variation in teeth on dental margin and setation (only setal bases shown on one side). A, B, F, NE QLD; E, SE QLD; C, D, G, H, New South Wales. Scales 0.25mm; scale for A applies to C-F, scale for B applies to G, H. A, QMS45174, Mt Fisher; B, QMS45116, The Bluff, W Mossman; C, QMS45193, Victoria Park via Alstonville; D, AM KS68724, Border Ranges NP; E, QMS45190, Mary Cairncross Park via Maleny; F, QMS45135, Mt Murray Prior; G, AM KS68730, Dorrig NP; H, AM KS68732, Bulga SF.

9E, F), with row of shorter, simple setae in arthrodial membrane on each side of plumose setae (Fig. 9E).

Second maxilla. Coxosternite concave anteriorly, sternite represented by shallow, narrow, V-shaped depression. Inner surface of tarsus fringed with long, large plumose setae; outer surfaces with evenly scattered simple setae (Fig. 9B); other articles of telopod bearing sparse simple setae (Fig. 9A). Pretarsal claw typically bears five digits: long, thick median digit, shorter lateral digits, needle-like intermediate digits (Fig. 9G).

Tergites (Fig. 2). T1 trapeziform, with marginal ridge entire, posterior rim raised; on TT3, 5, 8, 10, 12 marginal ridge entire, slightly raised, without median thickening. TT1 and 3 about equal in width; lateral borders of TT3 and 5 slightly convergent posteriorly, posterior angles rounded. T7 with parallel lateral borders, median

thickening of marginal ridge. T10 largest. Posterior border of T7 straight, that of TT1 and 8 straight or, more commonly, weakly concave; borders of TT3, 5, 10, 12 and 14 gently concave. Posterior angles of TT10 and 12 abruptly rounded; short subangular projections on TT11 and 13, smaller projection on T9; feeble, rounded posterior projection variably present on TT4 and 6. Posterior border of T14 and intermediate tergite concave in both sexes; intermediate tergite narrower in male, similarly sclerotised in both sexes. Tergites wrinkled; parallel rows of tubercles separated by longitudinal median furrow on TT(3) 5, 7, 8, 10 and 12; posterolaterally directed furrow across inner half of long tergites 3-12, radiating from front of median furrow; borders tuberculate.

Coxal pores. On legs 12-15; circular to oval, with continuous, raised rims, separated from each other by a space about equal to or less than their own diameter (Fig. 4D), set in shallow groove. Number of coxal pores tending to increase with size of specimen; maximum of 49 pores in total (female maximum 5,6,7,6 + 5,6,7,7, male maximum 5,6,7,6 + 4,7,6,6); larger specimens (width of head >1.7mm) usually with a combination of 4, 5 and 6 coxal pores,

exceptionally 3 or 7 on one or two legs. Usual sexual dimorphism in number of coxal pores, with females having slightly higher pore counts.

Legs. Tarsal articulation distinct on all legs; accessory apical claw on legs 14 and 15 nearly half length of principal claw, which is long, slender (Fig. 4G, H). Sensory spurs absent. Legs 14 and 15 thickened in both males and females, without sexual dimorphism; gradual increase in size of legs along length of body (Fig. 2); anal leg approximately 1/3 to slightly less than 1/2 length of body. Dense glandular pores on femur, tibia and basitarsus of legs 13-15. Plectrotaxy as shown in Table 1 (NE QLD) and Table 2 (New South Wales); variable spurs that are usually present: leg 11 (VmP), leg 13 (VpF, DaT), leg 14 (Vmt, VpF, DpF), leg 15 (VmP).

Female. First genital sternite with weak longitudinal median desclerotised strip. Gonopods with elongate, conical to

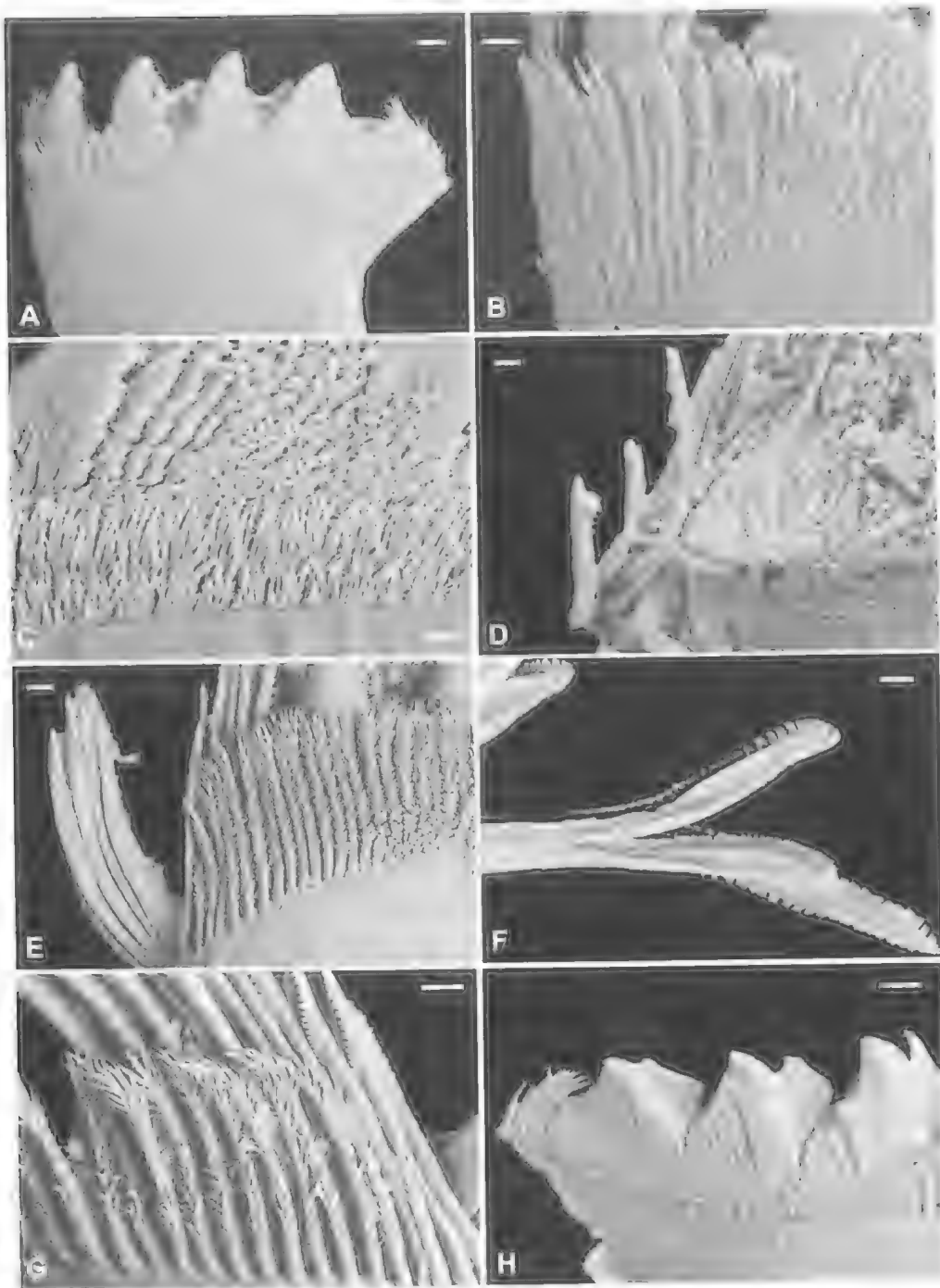


FIG. 8. *Australobius scabrior* Chamberlin, 1920. SEMs of mandibles. A-D. AM KS68718, ♀, Mt Hypipamee NP, NE Qld. A, gnathal lobe, scale 20µm; B, fringe of branching bristles on ventral part of mandible, scale 20µm; C, fringe of branching bristles, scale 5µm; D, aciculae and cluster of spines on inner surface of gnathal lobe, scale 10µm. E, AM KS68725, ♂, Richmond Ra. SF, NSW. Aciculae and fringe of branching bristles on ventral part of mandible, scale 10µm. F-H, AM KS68721, ♀, Kenilworth SF, SE Qld. F, aciculae, scale 5µm; G, aciculae and fringe of branching bristles on ventral part of mandible, scale 10µm; H, dorsal three pairs of teeth and furry pad, scale 10µm.

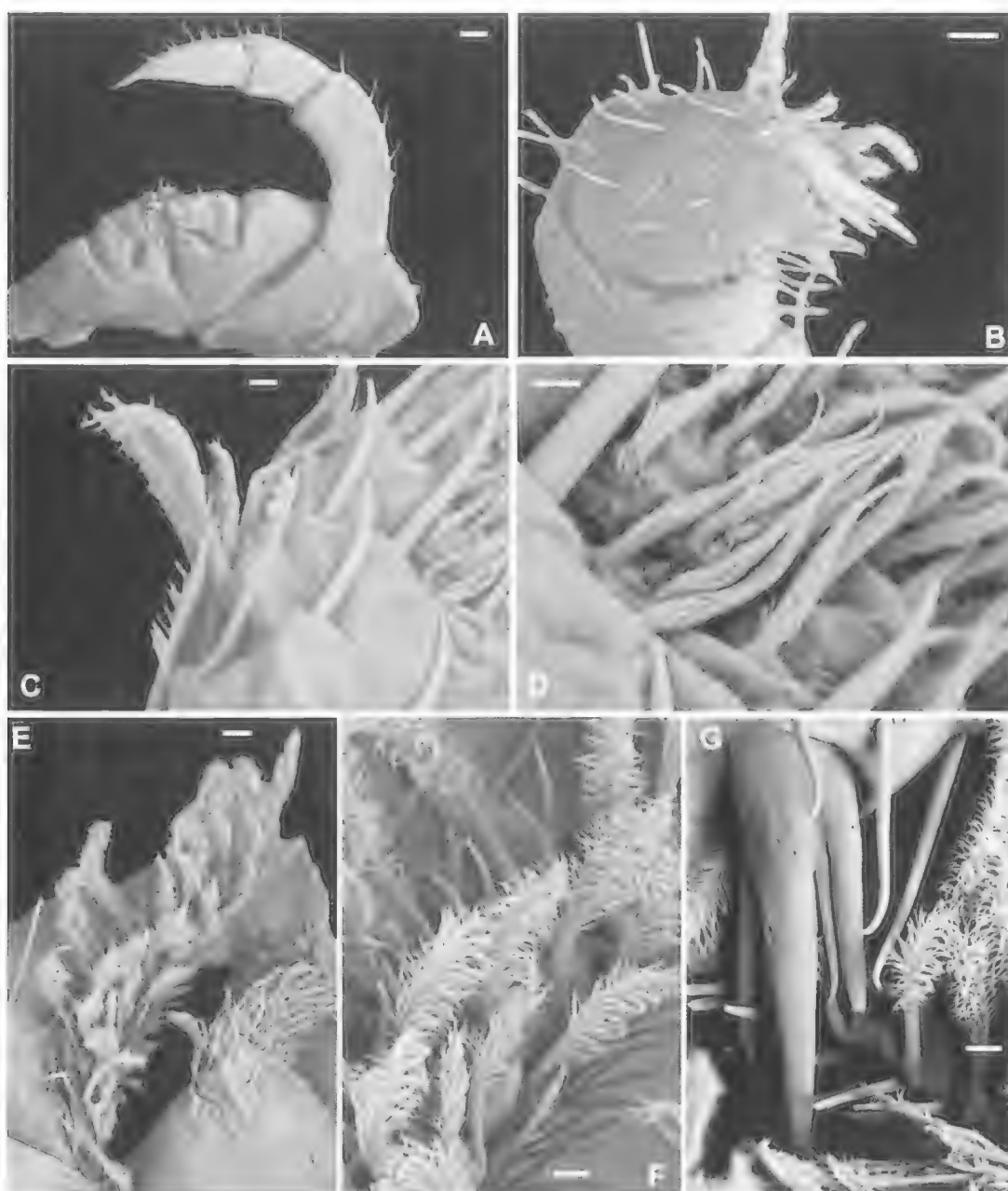


FIG. 9. *Australobius scabrior* Chamberlin, 1920. SEMs of maxillae. A, AM KS68718, ♀, Mt Hypipamee NP, NE Qld. First maxillae and second maxilla, scale 100µm. B-G, AM KS9356, ♀, Washpool NP, NSW. B, tarsus and pretarsus of second maxilla, scale 50µm; C, setae on coxal process of first maxilla, scale 5µm; D, complex setae on coxal process of first maxilla, scale 3µm; E, distal article of telopod and coxal process of first maxilla, scale 20µm; F, plumose setae on distal article of telopod of first maxilla, scale 10µm; G, pretarsus of second maxilla, scale 10µm.

bullet-shaped spurs (Figs 4F, 10); number of spurs on mature specimens most commonly 3+3 (Fig. 10A) or 4+4 (Fig. 10C), occasionally 5+5

(Fig. 10D); 2+2 spurs in immature specimens; innermost spur (when more than three present) shorter, more slender than others, other spurs

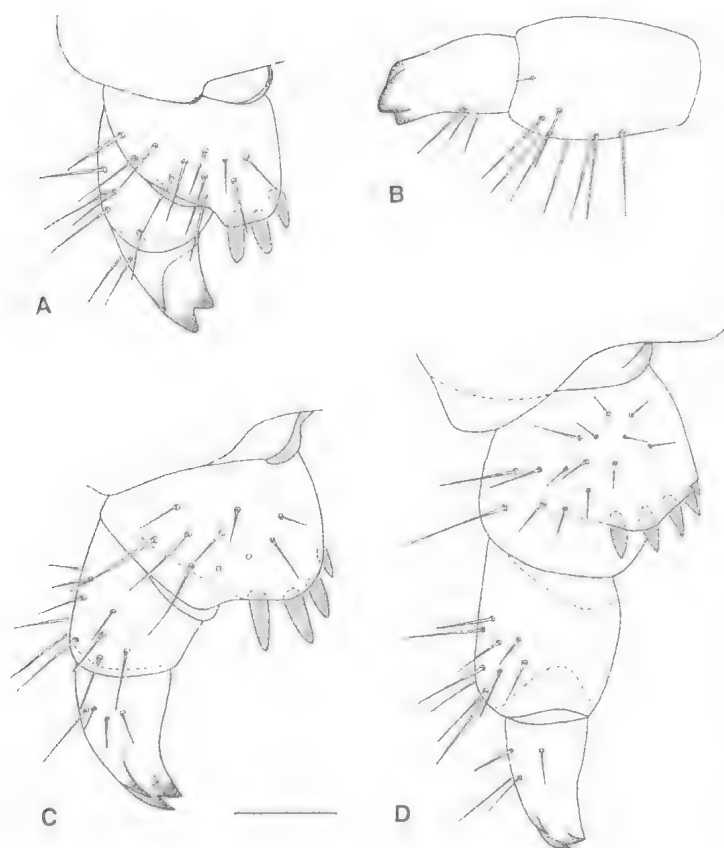


FIG. 10. *Australobius scabrior* Chamberlin, 1920. Female gonopods, showing variation in spur number. All ventral view except B, dorsolateral view. A, CAS, NE Eungella. B, C, QMS45117, The Bluff, W Mossman, NE QLD. D, QMS45175, Mt Father Clancy, NE QLD. Scale for all figures 0.25mm.

with slight increase in size from medial to lateral. First genital sternite and all articles of gonopods bear long, simple setae; setae evenly distributed on first genital sternite; 10-15 setae on basal article of gonopod, 5-10 on ventrolateral aspect of second article, tiny seta dorsolaterally near distal edge of article variably present (Fig. 10B), 2-4 setae on third article of gonopod. Claw tridentate, with both dorsal and ventral denticles distinct.

Male. First genital sternite bearing about 30 evenly scattered setae, longer on posterior part of sternite. Second genital sternite bearing two pairs of setae. Small gonopod of a single article, bearing one seta.

Larvae. Three larval stages correspond to 2-4 larval stages of *Lithobius variegatus* (Eason, 1964) or LII-LIV of *L. forficatus* (Andersson,

1976, table 1) with respect to leg and limb bud numbers.

Larva with 8 legs and two limb buds (LII) (QMS45141 - 45143): Length 3.1-3.7mm; width of head shield 0.53-0.55mm. 14 antennal articles. Two ocelli. 2 + 2 teeth on dental margin of maxillipede. Tarsal articulations indistinct.

Larva with 10 legs and two limb buds (LIII) (QMS45142, 45143): Width of head shield 0.58-0.59mm. 14 antennal articles. Two ocelli. 3+3 teeth on dental margin of maxillipede.

Larva with 12 legs and three limb buds (LIV) (QMS45091, 45093, 45096, 45141, 45143, 45146, 45150): Length 4.3-4.6mm; width of head shield 0.64-0.7mm. 17 antennal articles. Three ocelli. 3+3 teeth on dental margin of maxillipede. All tergites lacking projections. One coxal pore on leg 12.

DISCUSSION. The original description of *Australobius scabrior* was based on a single male, identifying the species using a small number of features, mainly: a general purple tinge; 21/22 antennal articles; large pale ocelli, the major ocellus being the largest, with an arrangement 1+2,2; dark, strongly chitinised maxillipede teeth with a 5+5

configuration; circular to weakly elliptical coxal pores of arrangement 3,5,5,4 (Chamberlin, 1920). Eason's (1996) description agreed with Chamberlin's except that his specimens had 20/21 antennal articles (an overwhelming majority of specimens in this study have 20); an arrangement of coxal pores of 3,4,5,4; and 4+5 teeth on the maxillipede. Eason indentified the prodont medial to the lateral tooth. The female gonopods were described as having 2+3 spurs and bidentate claws. The low spur number and absence of the third denticle on the claw may be accounted for by the size of the specimen; large females of *A. scabrior* consistently have a pair of accessory denticles on the gonopod claw.

All Australian material of *Australobius* is united by some diagnosible characters relative to non-Australian species (e.g., similar ocelli

TABLE 1. Plectrotaxy of *Australobius scabrior* based on several exemplar specimens from NE QLD. C = coxa, t = trochanter, P = prefemur, F = femur, T = tibia, a = anterior spur, m = median spur, p = posterior spur. Variable spurs indicated in parentheses.

Legs	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
1	-	-	p	(a)	(m)	-	-	amp	a	a
2	-	-	p	(a)(m)	m	-	-	amp	ap	a
3-5	-	-	p	am	(a)m	-	-	amp	ap	a
6	-	-	p	am	am	-	-	amp	ap	a
7-8	-	-	p	am	am	-	-	amp	ap	a
9	-	-	(m)p	am	am	-	-	amp	ap	a
10-11	-	-	(m)p	am	am	(a)	-	amp	ap	a
12	-	-	(a)mp	am	am	(a)	-	amp	ap	a
13	-	(m)	amp	am(p)	a(m)	(a)	-	amp	p	a
14	-	m	amp	amp	a	(a)	-	amp	(p)	-
15	-	m	amp	(a)m(p)	(a)	a	-	mp	-	-

distributions and shared position of the Tömösváry organ) and Australian *Australobius* may be regarded as a monophyletic group. However, several features that are routinely used to diagnose species in *Australobius* are variable within the Australian sample, and some exhibit distinct geographic trends. Perhaps the most conspicuous variation pertains to the number of teeth on the dental margin of the maxillipede. Accounting for the general trend towards an increase in tooth number ontogenetically, the range in large specimens is from four teeth per margin to 10 (Figs 7, 11). In general, specimens from the southern part of the range have more teeth: specimens from New South Wales often have six to eight teeth per margin (Fig. 7D,G), whereas those from north QLD commonly have five teeth per margin (Fig. 7B). This character

does not, however, permit a consistent basis for distinguishing the samples geographically, as some QLD specimens have higher tooth counts (Figs 7F, 11) whereas some from NSW have only five teeth (Fig. 7C). Tooth number is variable within single populations. Samples for which numerous large specimens are available show a range from 4+4 to 6+6 teeth (QMS45080, NE QLD), 4+4 to 7+7 teeth (QMS45135, NE QLD) and 5+5 to 6+7 teeth (AM KS68721, SE QLD). The total range in maxillipede dentition in *A. scabrior* is similar to that recorded in reared samples of *Lithobius forficatus* by Andersson (1976) (5+4 to 10+8 teeth per margin in the most mature stage, PL9).

Ocellus arrangements also display slight geographic variation (Fig. 5). Specimens from

TABLE 2. Plectrotaxy of *Australobius scabrior* based on several exemplar specimens from New South Wales. Abbreviations as in Table 1.

Legs	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
1	-	-	p	(a)(m)p	m	-	-	amp	a	a
2	-	-	p	(a)(m)p	(a)m	-	-	amp	ap	a
3-5	-	-	p	amp	(a)m	-	-	amp	ap	a
6	-	-	p	amp	am	-	-	amp	ap	a
7-8	-	-	p	amp	am	(a)	-	amp	ap	a
9-10	-	-	p	amp	am	(a)	-	amp	ap	a
11	-	-	(m)p	amp	am	(a)	-	amp	ap	a
12	-	-	(a)mp	amp	am	a	-	amp	ap	a
13	-	(m)	a(m)p	am(p)	a(m)	a	-	amp	(a)p	(a)
14	-	(m)	amp	am(p)	(a)	a	-	amp	(p)	(a)
15	-	m	a(m)p	(a)m(p)	(a)	a	-	(a)mp	-	-

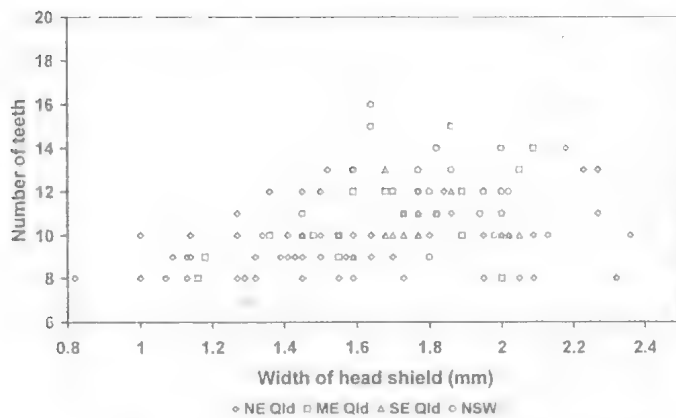


FIG. 11. Graph of number of teeth on dental margin of maxilliped, size (width of head shield used as proxy for body size) and geographic occurrence for *Australobius scabrior*.

the Wet Tropics region of NE QLD most commonly have a total of five ocelli in the two rows of seriate ocelli (Fig. 5A,B), though some have six (Fig. 5C). Most specimens from Cape York as well as NSW (Fig. 5I-L) have six ocelli in these two rows, though some have five. Specimens from ME QLD (Fig. 5D,E) and SE QLD (Fig. 5F-H) have a more even mix of either five or six seriate ocelli.

The number of spurs on the female gonopod in large specimens ranges from 3+3 to 5+5 across the samples from each of NE QLD, ME QLD and NSW (3+3 to 4+5 in SE QLD), though the frequency of different spur counts shows some geographic variation. Specimens from NE QLD have a similar representation of 3+3 and 4+4 spurs, whereas in specimens from SE QLD and NSW 4+4 spurs are considerably more common.

With respect to plectrotaxy, Australian *Australobius* displays considerable variability (Tables 1,2), again with some discernible geographic patterns. For example, specimens from NSW reach the anterior dispersional limit (Crabill, 1962) of the DaC spur on leg 7, and all specimens from New South Wales have this spur present on at least legs 12-15 (the anteriormost DaC on leg 7 is most common in New South Wales, but an anteriormost spur on any of legs 7-12 is observed). In samples from SE QLD, DaC is on legs 10-15 to 14-15. Most specimens from NE QLD have DaC restricted to legs 13-15 or 14-15, and sometimes confined to leg 15. These geographic trends are not consistently expressed, some NE QLD specimens having an anterior dispersional limit

of DaC on leg 10, farther forward than in some NSW specimens.

Another spur series that displays marked variation with respect to its anterior dispersional limit is VpF. Specimens from New South Wales and SE QLD have VpF on all trunk legs, whereas specimens from NE QLD typically lack VpF on legs 1-12. However, specimens from Eungella (ME QLD) have VpF with an anterior dispersional limit of leg 4. As well, specimens from NSW and SE QLD have VaT on legs 2-14 versus legs 6-14 in ME and NE QLD.

The inconsistent cline-like variation displayed by such features as maxilliped dentition and anterior dispersional limits of the DaC and VpF spurs is most readily interpreted as geographic variation in a native species. Accordingly, we consider Eason's (1974) speculation that *Australobius scabrior* could be a synanthropic introduction in Australia to be improbable.

Many species of *Australobius* have been based on small samples, in several cases only the holotype, sometimes without illustration. The degree of intraspecific variation observed in *A. scabrior* cautions that species distinguished by slight differences in maxilliped tooth number or female gonopod spur number are of dubious validity when they fall within the morphological range of *A. scabrior*. Many species require revision before their status can be further evaluated, several of the species named from New Guinea falling into this category. Four species of *Australobius* have been described from New Guinea: *A. lorae* (Silvestri, 1894), *A. viduus* Attems, 1932, *A. ethodes* (Chamberlin, 1939) and *A. tenuiunguis* Eason, 1980, each based on only one or a few specimens. Only *A. tenuiunguis* has been illustrated and thoroughly described. The types of *A. tenuiunguis* are from the Star Mountains. We have examined an additional, new specimen of this species, a male from the Highland Highway near Komum, Papua New Guinea, with 9+10 teeth on the dental margin of the maxilliped (ANIC Berlese sample 418, G. Baker, 16.vii.1972). *A. scabrior* is easily distinguished from *A. tenuiunguis* by its shorter antenna, without the elongate, tubular articles of the latter species, and *A. scabrior* has a substantially more tuberculate tergum and lacks

median thickenings of the marginal ridge on the long tergites except for T7.

Some samples from eastern Papua New Guinea in the Australian National Insect Collection (ANIC Berlesate 384, near Kokoda, c. 500m; ANIC Berlesate 393, "Timber Track", 16km NW Lae, c. 220m) include *Australobius* specimens that do not present obvious distinctions from *A. scabrior* specimens from Cape York or the Wet Tropics. Study of larger collections from PNG is required before the specific status of these specimens can be determined with confidence.

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LITERATURE CITED

- ANDERSSON, G. 1976. Post-embryonic development of *Lithobius forficatus* (L.), (Chilopoda: Lithobiidae). *Entomologica scandinavica* 7: 161-168.
- ATTEMS, C. 1932. Myriopoden. Resultats scientifiques du Voyage aux Indes orientales néerlandaises de LL. AA. RR. le Prince et la Princesse Léopold de Belgique. *Mémoires du Musée Royal d'Histoire naturelle de Belgique* (Hors Série) 3: 1-34.
- CHAMBERLIN, R.V. 1920. The Myriopoda of the Australian Region. *Bulletin of the Museum of Comparative Zoology at Harvard College* 64: 1-269.
1939. On a collection of chilopods from the East Indies. *Bulletin of the University of Utah, Biological Series* 5: 1-19.
- CRABILL, R.E., Jr. 1962. Plectrotaxy as a systematic criterion in lithobiomorphic centipedes (Chilopoda: Lithobiomorpha). *Proceedings of the United States National Museum* 113: 399-412.
- EASON, E.H. 1964. Centipedes of the British Isles. p.164 (F. Warne & Co.: London).
1974. On certain aspects of the generic classification of the Lithobiidae, with special reference to geographical distribution in Myriapoda. *Symposia of the Zoological Society of London* 32: 150-175.
1978. On Lithobiidae from the Seychelles with the descriptions of two new species of the subgenus *Australobius*, genus *Lithobius* (Chilopoda: Lithobiomorpha). *Journal of Zoology* 184: 21-34.
1980. Zoological results of the British Speleological Expedition to Papua New Guinea, 1975. A new species of the subgenus *Australobius*, genus *Lithobius* (Chilopoda: Lithobiomorpha) from Papua New Guinea. *Myriapodologica* 1: 41-46.
1986. The Lithobiidae of Thailand with descriptions of six new species of *Lithobius* and a new subspecies of *Australobius feae* (Pocock, 1891) (Chilopoda: Lithobiomorpha). *Steenstrupia* 12: 129-151.
1989. Lithobiidae from the Nepal Himalayas with descriptions of ten new species of *Lithobius* and *Australobius* (Chilopoda: Lithobiomorpha). *Zoologische Jahrbücher, Abteilung für Systematik* 116: 335-372.
1992. On the taxonomy and geographical distribution of the Lithobiomorpha. *Berichte des Naturwissenschaftlich-Medizinischen Vereins in Innsbruck Supplement* 10: 1-9.
1993. Descriptions of four new species of *Lithobius* from the Oriental Region and a redescription of *Australobius palnis* (Eason, 1973) from Sri Lanka. *Bolletino del Museo civico di Storia Naturale di Verona* 17 (1990): 181-200.
1996. The rediscovery of *Australobius scabrior* Chamberlin (Chilopoda: Lithobiidae). *Australian Entomologist* 23: 91-92.
1997. On some Lithobiomorpha from the mountains of Kirghizia and Kazakhstan (Chilopoda). *Arthropoda Selecta* 6: 117-121.
- EDGECOMBE, G.D., GIRIBET, G. & WHEELER, W.C. 2002. Phylogeny of Henicopidae (Chilopoda: Lithobiomorpha: Henicopidae): a combined analysis of morphology and five molecular loci. *Systematic Entomology* 27: 31-64.
- SILVESTRI, F. 1894. Chilopodi e Diplopodi della Papuasias. *Annali del Museo civico di Storia Naturale di Genova* 34: 619-659.

FISH FAUNA OF THE BENSBACH RIVER, SOUTHWEST PAPUA NEW GUINEA

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During anthropological research in the Bensbach river area of far southwestern Papua New Guinea, 1995-2000, an inventory of fish species in the river yielded 40 species. Taken together with other records and collections from the area a total fish population of at least 63 species is postulated. □ *Fish, species, Bensbach River, Papua New Guinea.*

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The distribution of New Guinea's freshwater fishes is very much correlated with the island's geology. There are two main zoogeographic provinces — a northern and a southern, divided by the central highlands. The southern is more speciose, reflecting a long and relatively stable geological history. In addition to a number of endemic fishes, the province also shares some 33 species with northern Australia, on account of the recent land connection between the two areas. This low-lying land bridge was inundated during the Holocene marine transgression, which created Torres Strait some 6,000-8,000 years ago (Allen, 1991; Jennings, 1972).

As Hyslop (1996) noted, our knowledge of New Guinea freshwater ichthyofauna is somewhat limited and is mainly focused on major river systems. For the southern province, information on fish species composition exists for the Fly (Roberts, 1978) and several systems further east: the lower and upper Purari (Haines, 1979, 1983; Allen & Jebb, 1993); the Brown, Goldie and Laloki (Berra et al., 1975); and the Angabanga (Hyslop, 1996).

Between 1995 and 2000 anthropological research was conducted on the environmental knowledge and subsistence systems of the people of the Bensbach River area in the Western Province, Papua New Guinea (PNG). As part of this research, an inventory of the fish species in the river was compiled.

THE BENSBACH RIVER AREA

The Bensbach River, also known as the Torassi, is a highly sinuous river situated in the extreme southwest corner of PNG (refer SC-54 Torres Strait 1:1,000,000 topographic map sheet for location of places mentioned in text). The mouth of the river marks part of the international

boundary with the Indonesian province of West Papua (141°01'10" E).

The environment of southwest PNG is unique in the country: It is wide, low and flat, and the landscape — savanna and seasonal wetlands — strongly resembles that of coastal and adjacent areas of northern Australia. The area experiences a monsoonal or tropical savanna climate, with approximately 75% of annual rainfall (1,682mm for Morehead) falling during a December to May wet season (Paijmans et al., 1971; Waithman, 1979). Much of the middle and lower Bensbach area is inundated during the wet season, on account of poor drainage characteristics and water draining into the area from higher rainfall areas to the north (Paijmans et al., 1971). In the dry season most of the area dries out as the waters gradually recede via a network of channels, although lagoons, small lakes and swamps remain in places. As the dry season progresses, tidal action pushes salt water approximately 100km upstream.

METHODS

The fish inventory was compiled using previous research (Allen, 1991; pers. comm. 1998); observation and collection of villagers' fish captures; and interviews using pictures (Whitehead, 1995). Villagers were also asked to collect any non-economic species they encountered while fishing. I also utilised the following techniques to collect fish: blocking of small swamp drainage channels flowing into the river at the end of the wet season using a fine mesh net; night fishing along the banks of the river using a pronged spear and torch; and shooting of fish using .22 rounds.

The majority of the fish were collected in the middle Bensbach area. Only two specimens were collected or identified near the river mouth. *Peri-*

ophthalmus novaeguineensis and *Periophthalmodon freycineti*. *Periophthalmus novaeguineensis* was observed at the mouth of the Bensbach River, but the voucher specimen was collected from the mouth of the Morehead River, the next river to the east.

Specimens were preserved in 10% formalin or 90% ethanol solutions. Identifications were made with reference to Allen (1991); further identifications of collected specimens and photographs of fish were made in Australia by staff of the Western Australian Museum, Perth (WAM), and Queensland Museum, Brisbane (QM).

RESULTS

I identified 40 fish species from the Bensbach River in the period 1995-2000. Twenty-three specimens have been deposited as voucher specimens in the Western Australian and Queensland Museums (Table 1).

Jerry Allen of the Western Australian Museum visited the middle Bensbach River in 1982 (29 September-1 October) and collected 32 species now housed at the Western Australian Museum (Allen, pers. comm. 1998). Of the fishes he collected I encountered 19; 13 were not: *Nematalosa erebi*, *Pseudomugil gertrudae*, *P. tenellus*, *Ophisternon gutturale*, *Ambassis macleayi*, *Pingalla lorentzi*, *Glossamia narindica*, *Liza macrolepis*, *Hypseleotris compressa*, *Oxyeleotris ariensis*, *Oxyeleotris paucipora*, *Glossogobius* sp. and *Redigobius bikolanus*.

As at 1975 the fish reference collection at the Kanudi Fisheries Research Laboratory in Port Moresby held 10 species from the Bensbach River. These were collected in October 1969 and May-June 1970 (Kailola, 1975). Of these, *Ambassis interruptus*, *A. nalua* and *A. urotaenia* (identified as *A. commersoni* in Kailola (1975), this specimen is most likely *A. urotaenia* [Jerry Allen, pers. comm. 2000]) were the only species

TABLE 1. Checklist of the Fishes of the Bensbach River. V = voucher specimen, P = specimen identified from photograph held by author.

Family Species	GH 1995-2000	Allen 1982	Kanudi 1969-1970
Indigenous Species			
Carcharhinidae – sharks			
<i>Carcharhinus leucas</i>	P		
<i>Carcharhinus amboinensis</i>	P		
Pristidae – sawfish			
<i>Pristis microdon</i>	P		
Osteoglossidae – saratoga			
<i>Scleropages jardinii</i>	P	V	V
Megalopidae – tarpons			
<i>Megalops cyprinoides</i>	P		
Clupeidae – herrings			
<i>Nematalosa erebi</i>		V	
Engraulidae – anchovies			
<i>Thyssa scratchleyi</i>	P	V	
Ariidae – fork-tailed catfishes			
<i>Arius graeffei</i>	QMI37105	V	
<i>Arius leptaspis</i>	WAMP.31342-006		
Plotosidae – eel-tailed catfishes			
<i>Neosilurus ater</i>	P	V	
<i>Porochilus meraukensis</i>	WAMP.31380-002		
Belonidae – longtoms			
<i>Strongylura krefftii</i>	P		
Melanotaeniidae – rainbowfishes			
<i>Iriatherina werneri</i>	WAMP.31342-010	V	V
<i>Melanotaenia maccullochi</i>	WAMP.31342-008	V	
<i>Melanotaenia splendida rubrostriata</i>	WAMP.31342-013	V	V
Pseudomugilidae – blue-eyes			
<i>Pseudomugil gertrudae</i>		V	
<i>Pseudomugil tenellus</i>		V	
Atherinidae – hardyheads			
<i>Craterocephalus randi</i>	WAMP.31342-007 WAMP.31380-006	V	V
Synbranchidae – swamp eels			
<i>Ophisternon bengalense</i>	WAMP.31342-005	V	
<i>Ophisternon gutturale</i>			
Centropomidae – barramundi			
<i>Lates calcarifer</i>	P	V	
Ambassidae – glass perchlets			
<i>Ambassis agrammus</i>	WAMP.31342-012	V	
<i>Ambassis interruptus</i>	WAMP.31380-005		V
<i>Ambassis macleayi</i>		V	V
<i>Ambassis nalua</i>		V	V
<i>Ambassis urotaenia</i>	WAMP.31342-011	V	V
<i>Denariusa bandata</i>	P	V	V
<i>Parambassis gulliveri</i>			

not collected by Allen or myself. Details of specimens that may have been added to it since 1975 are currently not available (Ursula Kolkolo, National Fisheries Authority, pers. comm. 1999).

When my inventory is combined with that of Allen (unpubl. data) and the Kanudi fish reference collection, a total of 56 species are known to occur in the Bensbach River.

DISCUSSION

The number of fishes known from the Bensbach River is similar to other river systems in southern Papua New Guinea. Hyslop (1996) found 43 fish species in the Angabanga River; Haines (1979) found 51 in the Purari; and Berra et

TABLE 1 (cont.)

Family Species	GH 1995-2000	Allen 1982	Kanudi 1969-1970
Terapontidae – grunters			
<i>Amniataba affinis</i>	P	V	
<i>Hephaestus raymondi</i>	WAMP.31342-001		
<i>Pingalla lorentzi</i>		V	
<i>Variichthys lacustris</i>	WAMP.31342-002		
Apogonidae – mouth-almighties			
<i>Glossamia aprion</i>	WAMP.31340-001	V	
<i>Glossamia nardica</i>	WAMP.31342-003	V	
Danioideidae – tigerfishes			
<i>Coius campbelli</i>	P		
Toxotidae – archerfishes			
<i>Toxotes chatareus</i>	P	V	V
<i>Toxotes lorentzi</i>	WAMP.31380-003		
Mugilidae – mullets			
<i>Lei macrolepis</i>		V	
<i>Lei subviridis</i>	P	V	
Eleotrididae – gudgeons			
<i>Hypseleotris compressa</i>		V	
<i>Mogurnda mogurnda</i>	WAMP.31341-001 WAMP.31381-001		
<i>Oxyeleotris aruensis</i>		V	
<i>Oxyeleotris fimbriata</i>	P	V	
<i>Oxyeleotris herwerdenii</i>	WAMP.31341-002 WAMP.31380-001	V	
<i>Oxyeleotris nullipora</i>	WAMP.31342-009 WAMP.31381-002	V	
<i>Oxyeleotris paucipora</i>		V	
Gobiidae – gobies			
<i>Glossogobius</i> sp.		V	
<i>Redigobius bikolanus</i>		V	
<i>Periophthalmus novaeguineensis</i>	WAMP.31382-001		
<i>Periophthalmodon freycineti</i>	QMI31074		
Kurtidae – nurseryfishes			
<i>Kurtus gulliveri</i>	QMI31073		
Soleidae – soles			
<i>Aseraggodes klunzingeri</i>	WAMP.31342-004	V	
Non-indigenous Species			
Clariidae – walking catfishes			
<i>Clarias batrachus</i>	WAMP.31341-003		
Cichlidae – cichlids			
<i>Oreochromis mossambica</i>	P		
Anabantidae – climbing perches			
<i>Anabas testudineus</i>	WAMP.31380-004		
Channidae – snakeheads			
<i>Channa striata</i>	P		

al. (1975) found a combined total of 43 species for the Brown, Laloki and Goldie Rivers. Fifty-five species of freshwater fish have been collected in Kakadu National Park in the Northern Territory of Australia, a similar wetland environmental area (Press et al., 1995). Of these, 25 are shared with the Bensbach River system.

Local people interviewed about the river's fishes, using the pictures in Allen (1991) as a guide (Whitehead, 1995), stated that a number of additional species are present in the Bensbach. At least twenty additional freshwater fish species are known to occur in other rivers of central-southern New Guinea (Allen, 1991). On the basis of this distribution of fishes, Osborne

(1993, pers. comm. 1999) has suggested that some 63 species may occur in the Bensbach River. As most of the species collected here and by Allen are from the middle Bensbach, it is recommended that further collecting be undertaken in the lower and upper reaches of the system, as well as the creeks and permanent swamps. It is probable that this will add to the total number of fishes known from the system.

Local people also identified significant recent impacts on the Bensbach River fishery linked to environmental changes and introduced species. Javan Rusa deer (*Cervus timorensis*), an introduced species which first entered this part of the Western Province in the late 1940s/early 1950s, have destroyed much of the riverbank grasses and permanent swamps in the area through overgrazing and trampling. According to the local people, the destruction of much of this habitat has resulted in a marked decline of certain species, such as eleotridids.

Four of the species collected are recent exotic introductions from the Merauke area in southeast West Papua: *Anabas testudineus*, *Oreochromis mossambica*, *Clarias batrachus* and *Channa striata*. All have entered the system via human

vectors, namely transmigrants from other parts of Indonesia who have brought their food fishes with them to the West Papua border area. Government records at Balamuk village indicate that *A. testudineus* was first encountered in the Weam area of the Bensbach in 1985, possibly entering the river via drainage ditches associated with the building of the Trans-Irian Highway, which in 1982 crossed the international border in two locations near the upper Bensbach River (May, 1986). *O. mossambica* and *C. batrachus* are more recent introductions, first encountered by villagers on the middle Bensbach around 1995. Two specimens of *C. striata* observed by the author in August 2000 at Balamuk and Wando

villages were among the first of this species to be caught by local people. This species is regarded as a particularly voracious predator of native fish (Allen, 1991). The recent introduction and rapid spread of these fishes is a grave threat to the biosecurity of this and other freshwater ecosystems in Papua New Guinea, and warrants further monitoring and research.

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LITERATURE CITED

- ALLEN, G.R. 1991. Field guide to the freshwater fishes of New Guinea. (Christensen Research Institute: Madang).
- ALLEN, G.R. & JEBB, M. 1993. A collection of fishes from the upper Purari River system, Papua New Guinea, with descriptions of two new species (Terapontidae and Eleotrididae). *Ichthyological Exploration of Freshwaters* 4: 289-304.
- BERRA, T.M., MOORE, R. & REYNOLDS, L.F. 1975. The freshwater fishes of the Laloki river system of New Guinea. *Copeia* 2: 316-326.
- HAINES, A.K. 1979. An ecological survey of fish of the lower Purari River system Papua New Guinea. In Petr, T. (ed.) *Purari River (Wabo) hydroelectric scheme environmental studies*, 6. (Office of Environment and Conservation: Waigani).
1983. Fish fauna and ecology. In Petr, T. (ed.) *The Purari – tropical environment of a high rainfall river basin*. (Junk: The Hague).
- HYSLOP, E.J. 1996. Species composition of the fish catch from the Angabanga River, Papua New Guinea. *Science in New Guinea* 22(1): 3-8.
- JENNINGS, J.N. 1972. Some attributes of Torres Strait. Pp. 29-38. In Walker, D. (ed.) *Bridge and barrier: the natural and cultural history of Torres Strait*. (Australian National University: Canberra).
- KAILOLA, P.J. 1975. A catalogue of the fish reference collection at the Kanudi Fisheries Research Laboratory, Port Moresby. Department of Agriculture, Stock & Fisheries Research Bulletin No.16.
- MAY, R.J. 1986. East of the border: Irian Jaya and the border in Papua New Guinea's domestic and foreign politics. Pp. 85-160. In May, R.J. (ed.) *Between two nations: the Indonesia-Papua New Guinea border and West Papua nationalism*. (Robert Brown and Associates: Bathurst).
- OSBORNE, P.L. 1993. Biodiversity and conservation of freshwater wetlands in Papua New Guinea. Pp. 327-380. In Beehler, B.M. (ed.) *Papua New Guinea conservation needs assessment*, Vol. 2. (Government of Papua New Guinea, Department of Environment and Conservation: Boroko).
- PAIJMANS, K., BLAKE, D.H., BLEEKER, P. & McALPINE, J.R. 1970. Land resources of the Morehead-Kiunga area. Territory of Papua and New Guinea. CSIRO Land Research Series 29.
- PRESS, T., LEA, D., WEBB, A. & GRAHAM, A. 1995. Kakadu: natural and cultural heritage and management. (Australian Nature Conservation Agency and North Australia Research Unit, The Australian National University: Darwin).
- ROBERTS, T. 1978. An ichthyological study of the Fly River Papua New Guinea with descriptions of new species. *Smithsonian Contributions to Zoology* No. 281.
- WHITEHEAD, H. 1995. Identifying game species with the aid of pictures in Papua New Guinea. *Pacific Studies* 18: 1-38.

A SPECIMEN RECORD OF WHITE-BELLIED STORM-PETREL FROM FRASER ISLAND, SOUTHEAST QUEENSLAND. *Memoirs of the Queensland Museum* 48(1): 123-124, 2002:- The White-bellied Storm-petrel (*Fregatta grallaria* Vieillot, 1817) lives in Southern Hemisphere subantarctic, subtropical and tropical waters (Marchant & Higgins, 1990). Four subspecies breed on isolated groups of islands and differ primarily in morphometries (Table 1). The nominate subspecies breeds on Admiralty Island (Roach), Lord Howe Is and Kennadee Group (Macaulay and Curtis Is.) and is the closest known form to E Australia. *F. g. leucogaster* is of similar size to *F. g. grallaria* and breeds on Tristan da Cunha Group, Ill St Paul and Amsterdam Is (Elliot, 1957; Jouventin, 1994.). *F. g. segethi* is small and breeds on Juan Fernandez Is (Marchant & Higgins, 1990). *F. g. titan* is the largest subspecies, breeding on central Pacific Rapa Is and the Austral Group (Murphy, 1928).

Breeding biology is poorly known; at Lord Howe Is. Egg-laying begins in late January- February (Hindwood, 1940) with offspring fledging in May (Mathews, 1928). *F. g. leucogaster* (Marchant & Higgins, 1990) and *F. g. segethi* (Bent, 1922) are also summer or late summer breeders. After breeding they disperse and become largely pelagic in subtropical and tropical waters feeding on cephalopods and crustaceans (Marchant & Higgins, 1990).

Status of the White-bellied Storm-petrel in Australia is poorly known; sight-records from the Coral Sea (Stokes & Corben, 1985), Tasman Sea (Norris, 1967), offshore St. Qld and NNSW (Marchant & Higgins, 1990) and inshore at Point Lookout, North Stradbroke Is. (Palliser, 1985); and a beach-washed specimen at Eaglehawk Neck, Tasmania in 1928 (Fletcher, 1947).

We describe a bird from 2km S of Poyungan Rocks, Fraser Island (25°25'S, 153°10'E) on 24 March 1999. The intermediate morph in good condition, Queensland Museum specimen Q31230 has uniform sooty black upperparts, with

white uppertail coverts producing a sharply demarked white band above the base of the tail. Upperwings including primaries uniform sooty black; secondaries dark sooty brown. Most feathers on upperparts and wings, including the main flight feather tracts, in advanced stage of wear; some feathers on the mantle black, with white tipping (i.e. freshly moulted) indicating beginning of a body moult.

Head, chin, throat and upper-breast grey-brown shading to a white lower breast and abdomen (Figs 1, 2). Chin and throat feathers uniform grey-brown to their bases. Flanks white with short dark barring and mottling; on the right hand side a dark mark from the flanks separating white uppertail coverts from the underbody. Lateral undertail coverts black with white tipping to the feathers, enclosing the white central under tail covers having broad dark bars; this dark barring and mottling indicating an intermediate phase bird. Undertail sooty dark brown. Undersurface of the primaries and secondaries sooty dark brown, with the underwing lining white. Underwing with a broad but irregular shaped blackish leading edge enclosing the white lining.

Bill black, with a distinct downward curve towards the tip. Legs and feet black; toes not extending beyond tip of the tail.

Discussion

The White-bellied Storm-petrel specimen found on Fraser Island is clearly a bird of the nominate sub-species, with all except the tail measurements falling within this subspecies range (Table 1). This measurement of the tail was taken by Queensland Museum staff and could not be remeasured due to specimen preparation. If accurate, however this tail measurement is only just out-side the range derived from the data quoted for the subspecies by Marchant & Higgins 1990, and should not change any conclusion of specific identification of the specimen. Intermediate morph White-bellied Storm-Petrels are known only from the nominate subspecies, with the Lord Howe Island Group being the only polymorphic population. On the Lord Howe Island



FIG. 1. Dorsal view of Q31230.



FIG. 2. Ventral view of QMO31230.

Group, the intermediate morph is uncommon, with the polymorphic ratio of light: intermediate: dark birds at 1:4:5 (van Tets & Fullagar, 1984).

Although occasionally recorded in pelagic waters on the east coast of Australia (reviewed in Marchant & Higgins, 1990), the White-bellied Storm-petrel reported here is the first substantiated specimen for mainland Australia.

Literature Cited

- BENT, A.C. 1922. Life histories of North America Petrels, Pelicans, and their Allies, Order Tubinares and Order Steganopodes. Bulletin U.S. National Museum 121:1-335.
- HINDWOOD, K.A. 1940. The birds of Lord Howe Island. *Emu* 40: 1-86.
- ELLIOTT, H.F.I. 1957. A contribution to the ornithology of the Tristan Da Cunha Group. *Ibis*, 99: 545-586.
- FLETCHER, J.A. 1947. Stray feathers: Tasmanian Notes. *Emu* 46: 394-395.
- MARCHANT, S. & HIGGINS, P.J. 1990. (eds) Handbook of Australian, New Zealand & Antarctic Birds: Vol. 1 Ratites to Ducks, Part A. (Oxford University Press: Melbourne).
- MATHEWS, G.M. 1928. The birds of Norfolk and Lord Howe Islands and the Australian South Polar Quadrant with additions to the 'Birds of Australia'. Pp.139. (Witherby: London).
- MURPHY, R.C. 1928. Birds collected during the Whitney South Sea expedition IV. *American Museum Novitates* 322: 1-5.
- NORRIS, A.Y. 1967. Seabirds observations from the south-west Pacific in the southern winter. *Emu* 67: 33-54.
- PALLISER, T. 1985. The Queensland Ornithological Society Bird Report, 1984. *Sunbird* 15: 45-70.
- JOUVENTIN, P. 1994. Les Populations d'oiseaux marins des T.A.A.F.: Resume de 20 Annees de Recherche. *Alauda* 62: 44-47.
- STOKES, T. & CORBEN, C. 1985. A survey of pelagic birds in the western Coral Sea and Great Barrier Reef. *Corella* 9: 25-29.
- VAN TETS, G.F. & FULLAGAR, P.J. 1984. The status of Australian seabirds. *Australian Seabird Group Newsletter*. 20:1-25.
- Rod Hobson, Queensland Parks and Wildlife Service, Fraser Island, PMB 10, MS 2173 Rainbow Beach 4581, Australia. Present Address Queensland Parks and Wildlife Service, PO Box 731, Toowoomba 4350, Australia; David Stewart, Queensland Parks and Wildlife Service, Conservation Resource Unit, PO Box 42, Kenmore 4069, Australia; received 24 May 2001.*

TABLE 1. Morphometrics of the four subspecies of White-tailed Storm-Petrels and the specimen from Fraser Island.

	<i>grallaria</i>	<i>leucogaster</i>	<i>segethi</i>	<i>titan</i>	QMO31230
Culmen	13.0-15.0	14.2-17.0	12.6-14.0	15.0-16.3	13.5
Bill depth					5.8
Bill width					5.7
Wing	159-176	158-182	146-163	177-188	175
Tail	66-82	71-90	71-77	78-89	84
Tarsus	35.1-39.6	37-43	33-37	39-43	36
Mid toe	20.2-23.4	22-30	20-22.6	23.6-27.0	21

COMPARATIVE MAXILLARY AND DENTARY MORPHOLOGY OF THE AUSTRALIAN DRAGONS (AGAMIDAE: SQUAMATA): A FRAMEWORK FOR FOSSIL IDENTIFICATION

SCOTT A. HOCKNULL

Hocknull, S.A. 2002 5 31: Comparative maxillary and dentary morphology of the Australian dragons (Agamidae: Squamata): A framework for fossil identification. *Memoirs of the Queensland Museum*. 48(1): 125-145, Brisbane. ISSN 0079-8835.

The maxilla, particularly its anterior portion, and dentary of extant Australian agamids, excluding *Cryptagama* and *Hypsilurus*, provide a framework for identification of fossil agamids. Juvenile agamids can be distinguished from adults on their pleurodont teeth relative to the first acrodon tooth, a posterior-most acrodon tooth that is the largest in the tooth row, and acrodon teeth with translucent margins. Sexual dimorphism occurs in *Ctenophorus maculatus*, *C. pictus* and *Tympanocryptis intima*, which have distinctly larger maxillary caniniform pleurodont teeth in males than in females. *Amphibolurus*, *Lophognathus*, *Caimanops*, *Chlamydosaurus* and *Diporiphora* share many features including, an angular dorsal maxillary process and reduced naris ridge. *Amphibolurus* shares most features with *Lophognathus gilberti* and *Lophognathus temporalis*. *Caimanops* is morphologically similar to *Chlamydosaurus*, but is smaller and *Diporiphora* is similar to *Amphibolurus nobbi*, but smaller. *Tympanocryptis* differs from *Rankinia* by its caniniform pleurodont dentition. The *Ctenophorus reticulatus* species group is closest to *Pogona*, possessing rounded maxillary and dentary acrodon dentition. *Physignathus* and *Chelosania* share more features with each other than with other Australian agamids. *Moloch* shares many features with *Tympanocryptis*, including the vertical dorsal maxillary process and angled maxillary acrodon teeth. Although *Moloch* has many derived features of the maxillae and dentary, it also has features of the more plesiomorphic *Physignathus* and *Chelosania*. □
Australian, Agamidae, comparative morphology, maxilla, dentary.

Scott Hocknull, Queensland Museum, PO Box 3300 South Brisbane 4101; received 14 February 2000.

Dragon (or agamid) lizards are a conspicuous group of Old World squamates, found in most Australian terrestrial environments. They exhibit a diversity of form and behaviour, which is paralleled only by their iguanian New World relatives. Frills, humps, beards, sails and facial ornamentation provide a range of external characters as the basis of most agamid species. However, external features are useless in identifying fossil agamids. This paper describes morphological variation in the maxilla and dentary of Australian agamid genera (except *Cryptagama* and *Hypsilurus*) as a framework for fossil identifications and phylogenetic reconstruction. Siebenrock (1895) was apparently the first to illustrate skulls of Australopapuan agamids; including *Moloch horridus*. Cogger (1961) used agamid skull morphology and morphometrics to define Australian taxa with neotenic characteristics. Mitchell (1965) considered osteological data to separate *Ctenophorus maculosus* from *Tympanocryptis*. Badham (1976) provided osteological data to separate species of *Pogona*.

Kent (1987) noted osteological features of *Rankinia diemensis*. Greer (1987, 1989a) described the postcranial osteology of *Ctenophorus clayi* and *Ctenophorus femoralis*. Greer (1989b) reviewed osteological knowledge of Australian agamids. Witten (1993) summarised the skeletal system of Australian agamids, noting that the general caniniform nature of agamid pleurodont dentition with specific reference to the extreme enlargement of the pleurodont dentition in *Chlamydosaurus* and *Tympanocryptis*. *Caimanops*, *Diporiphora*, *Ctenophorus pictus* and *Ctenophorus rufescens* all share equivalently large, caniniform pleurodont teeth. Examination of specimens in this study reveals some necessary modifications to earlier works: Covacevich et al., (1990, fig 1) in illustrating a series of Australian agamid maxillae and dentaries transposed captions to two figures (fig. 1g – *Caimanops amphiboluroides* = *Tympanocryptis tetraporophora*; fig. 1h – *Tympanocryptis tetraporophora* = *Caimanops amphiboluroides*; fig. 1i – *Ctenophorus caudicinctus* = *Lopognathus gilberti*; fig. 1j – *Lophognathus*

gilberti = *Ctenophorus caudicinctus*); Witten (1993: 243) noted "...*Moloch horridus* has lost the anterior pleurodont teeth...". *Moloch* specimens examined herein have 2-3 premaxillary, 3 maxillary and 3 dentary pleurodont teeth in each tooth row. Witten's (1993, fig 29.5B, C) skull drawing of *Hypsilurus boydii* represents specimens now identified as *Physignathus lesueurii* rather than *Hypsilurus boydii*.

An osteological framework for identification of modern and fossil agamids is lacking (Archer, 1978; Estes, 1985; Molnar, 1991; Molnar & Kurtz, 1997; Mackness & Hutchinson, 2000). Attempts to identify fossil agamids below family level, include Lydekker (1888) who identified *Chlamydosaurus kingii* from the eastern Darling Downs; Smith (1976) who identified *Amphibolurus* from the Naracoorte Caves, tentatively assigning them to *A. barbatus*, now *Pogona barbata*; and Covacevich et al., (1990) who identified *Physignathus* sp. and *Sulcatidens quadratus* (Fig. 1B, C), from the Oligocene-Miocene of Riversleigh, using maxillae and dentaries.

METHODS

Systematics for this study follow Cogger (2000) and Wilson & Knowles (1988) with a few modifications. Recognition of *Rankinia* follows Greer (1989b). *T. pinguicollis* was raised to species level by Smith et al. (1999) who used molecular data with little morphological and no osteological data, making it impossible to determine the comparative specimens referred to only as *T. lineata*. *T. lineata* and *T. pinguicollis* are treated as synonyms, until skins of the skeletons used in the present study can be properly identified. *Diporiphora* has been split into two groups based on maxillary pleurodont tooth count as a tool to differentiate species within this large genus. *Ctenophorus* species groups are based on external morphology (Wilson & Knowles, 1988). This allowed the greatest diversity of osteology to be analysed with at least one species within each of these species groups attained for the present study. Osteological data suggest that species groups should be combined, as in Witten (1982). However, this is reserved until a larger collection of skeletons is available.

At least one adult and one juvenile of each Australian agamid genus, except *Cryptagama*, have been examined to distinguish juveniles from adults. *Cryptagama* was not available for observation. *Hypsilurus* (Figs 8E, 9M) is illustrated but not described because it is to be included in a forthcoming review of Australian

and PNG agamids. Species variation has been noted where numerous skeletal and spirit specimens are available (e.g. *Chlamydosaurus kingii*, *Physignathus lesueurii* and *Pogona barbata*). Two or more adult skulls of each monotypic genus are available, except *Caimanops* where only 1 was available. For polytypic genera the numbers of skulls available were: *Amphibolurus* (7), *Ctenophorus* (58), *Diporiphora* (14), *Hypsilurus* (5), *Lophognathus* (10), *Pogona* (13), *Rankinia* (3), *Tympanocryptis* (9).

Variations in pleurodont and acrodon tooth counts, orientation, size and shape were noted on defleshed skulls and spirit specimens. Teeth on the latter can be examined by making a small labial incision and carefully peeling the scales back with a pair of fine forceps. Morphological features referred to herein are illustrated in Fig. 4.

Specimens (Appendix 1) are deposited in the Queensland Museum (QMJ), Museum and Art Gallery of the Northern Territory (NTR), Australian Museum (AMR), Western Australian Museum (WAMR), Muséum d'Histoire Naturelle (MNHN) and University of Michigan Museum of Zoology (UMMZ).

AGAMID OSTEOLOGY AND ONTOGENY

The most diagnostic skeletal feature of agamids, and their sister taxon the chameleons, is the acrodon dentition on maxilla and dentary (Cooper et al., 1970). This feature defines the Acrodonta (Frost & Etheridge, 1989), a group with Cretaceous ancestry (Moody, 1980). Agamids also possess anterior successional pleurodont teeth. Pleurodont teeth begin their eruption sequence with the egg tooth in the midline of the premaxilla. Throughout ontogeny pleurodont teeth are replaced by larger successors that either remain in their fixed position or are displaced by newly erupting pleurodont teeth posteriorly. In adults, eruption of the final pleurodont tooth series initiates wearing down of the tooth row. It is common to find a tooth row completely devoid of functional teeth, leaving the last few posterior acrodon teeth in each jaw.

Acrodon teeth erupt posteriorly and are never shed. Erupting pleurodont teeth push out anterior acrodon teeth, but the final acrodon tooth count does not change once the animal has matured. Acrodon teeth undergo varying amounts of wear depending on age of the lizard and position of the tooth. Anteriormost acrodon teeth are abraded first by occlusion with their counterparts. In subadults the posterior quarter of the tooth row

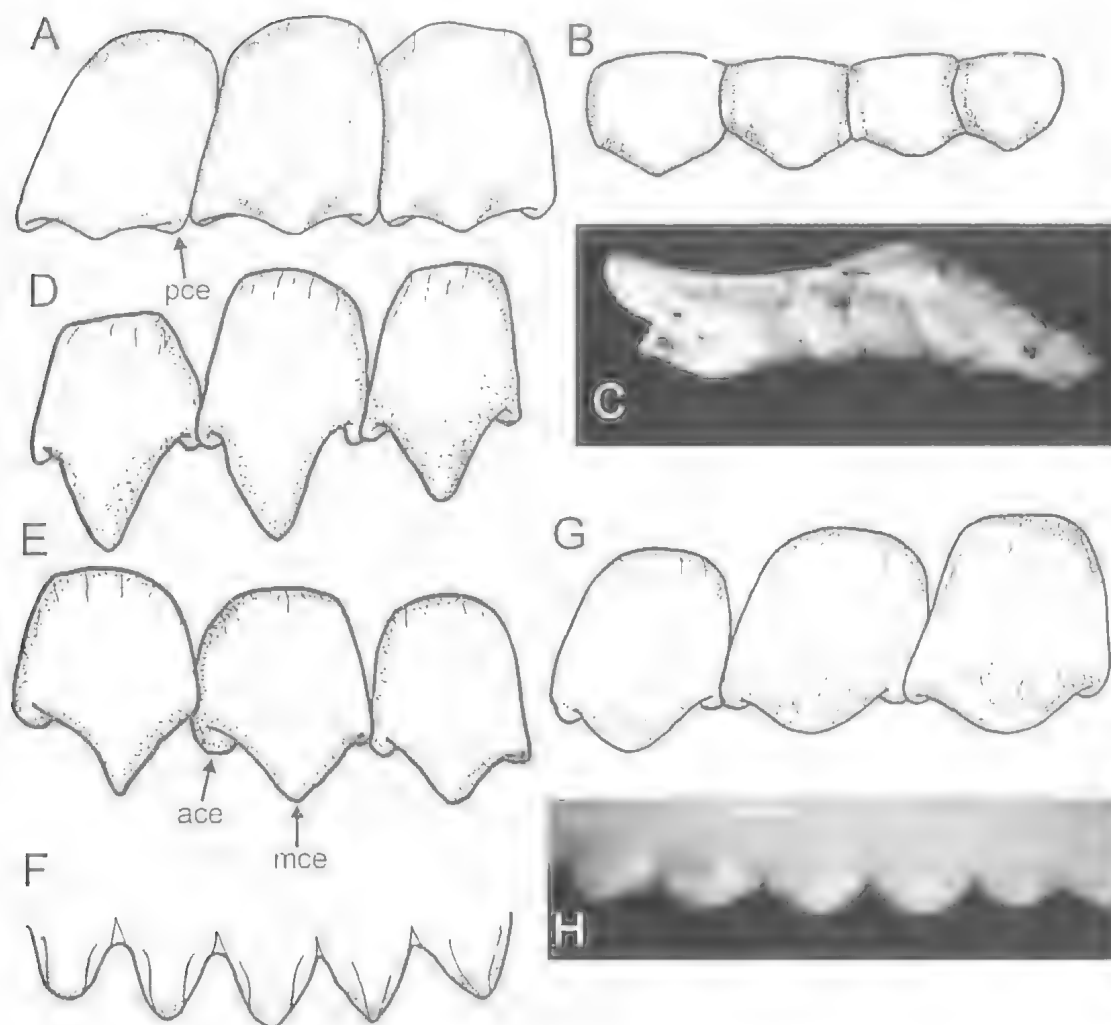


FIG. 1. Australian agamid maxillary acrodon tooth shapes. A, Quadrilateral-shaped (lingual view); B, Quadrilateral-shaped and socketed (labial view); C, Occlusal view; D, Mesocone dominant (lingual view); E, Antero-mesocone dominant (lingual view); F, Simple triangular (lingual view); G, Rounded (lingual view); H, Labial view. Abbreviations: pce; posterocone, ace; anterocone, mce; mesocone.

usually has little or no wear. In old individuals wear may obliterate the entire acrodon and pleurodon tooth row, leaving a toothless ridge of jaw.

The acrodon tooth in most Australian agamids looks triangular after a period of wear. If a jaw has unworn teeth - generally the last 2-3 - then relative size, morphology and orientation of the cusps can be used for identification.

TOOTH TERMINOLOGY AND VARIATION

Pleurodon (P) and acrodon (A) teeth have

their position along the tooth row indicated by a number in superscript for maxillary and subscript for dentary teeth. Acrodon teeth have 3 cusps variously expressed. To differentiate, the following terminology is used mirroring that for mammal teeth indicating upper and lower cusps: in the maxilla, the anterior cusp is the 'anterocone'; most prominent middle cusp is the 'mesocone'; and the posterior cusp is the 'posterocone'. In the dentary, the anterior cusp is the 'anteroconid'; middle, and most prominent, cusp the 'mesoconid'; and the posterior cusp the 'posteroconid' (Figs 1, 2).

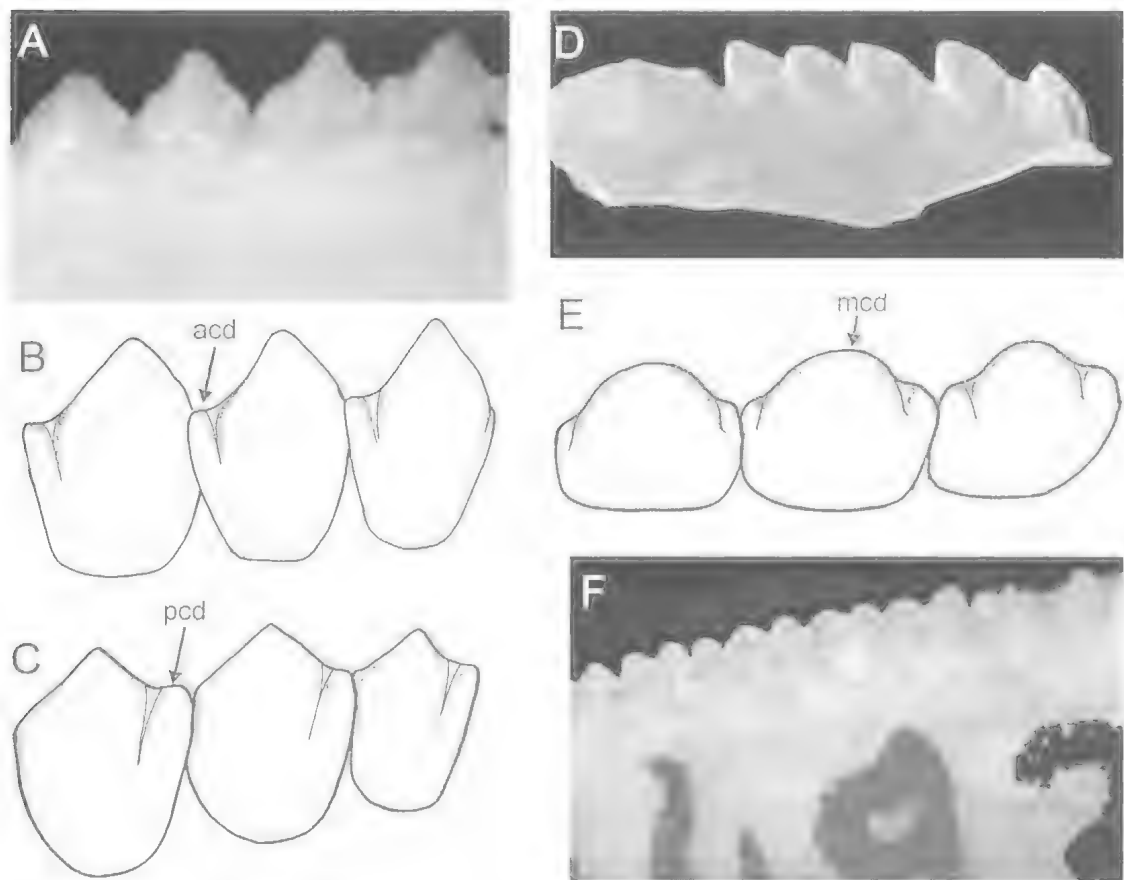


FIG. 2. Australian agamid dentary acrodont tooth shapes. A, Subtriangular (labial view); B, Anteroconid dominant (lingual view); C, Posteroconid dominant (lingual view); D, Recliné axis and crested (labial view); E, Rounded (lingual view); F, Tricuspid with labially displaced mesoconid (labial view). Abbreviations: acd; anteroconid, mcd; mesoconid, pcd; posteroconid.

Abbreviations. **acd**: anteroconid, **acc**: anterocone, **amh**: anterior maxillary height, **aml**: anterior maxillary length, **arl**: maxillary acrodont tooth row length, **darl**: dentary acrodont tooth row length, **dl**: dentary length, **dmk**: dorsal maxillary kink, **dmp**: dorsal maxillary process, **dmpw**: dorsal maxillary process width, **dms**: dorsal maxillary process slope, **ds**: dental sulcus, **ha**: hooked anterior margin, **ipmp**: inferior-posterior maxillary process, **jms**: jugal/maxillary suture, **lmf**: labial maxillary foramina, **mcd**: mesoconid, **mce**: mesocone, **mg**: Meckel's groove, **ml**: maxilla length, **n**: number of specimens, **pams**: palatine/maxillary suture, **pcd**: posteroconid, **pce**: posterocone, **pdd**: posterior dentary depth, **pfms**: prefrontal/maxillary suture, **pms**: premaxillary/maxillary suture, **spmp**: superior-posterior maxillary process, **sym**: symphysis.

JUVENILES

Spirit juveniles show variations not present in any adult form: 1) A gradation of acrodont tooth size from smallest anteriorly to largest posteriorly, the posteriormost tooth being largest. In adults there is a marked division of acrodont tooth size into 'premolars' and 'molars', with most having the posteriormost tooth not the largest. 2) In juveniles sutures were not closed and the bone had not matured, so that bones were fragile and marginally translucent. In adults there is complete ossification and the bone is opaque. 3) Pleurodont teeth in juveniles are the same size as, or smaller than, the first acrodont tooth. After being replaced by the next pleurodont tooth generation, the lizard assumes the adult tooth size and size difference. 4) Juvenile acrodont teeth are hollow, compared with the robust, solid acrodont

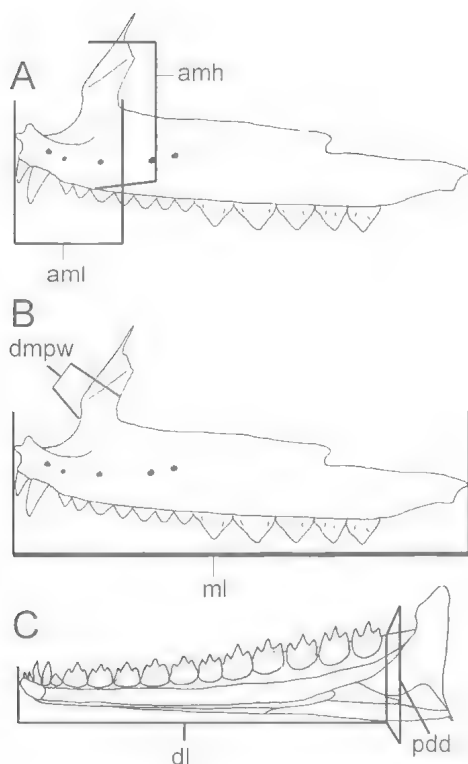


FIG. 3. Morphometric measurements taken for agamid maxillae and dentaries. A, B, Maxillary measurements; C, Dentary measurements.

teeth of adults. Sub-fossil juvenile agamid fragments from Henk's Cave, Lamington Plateau, *Physignathus lesueurii* and an unidentifiable specimen show the characters mentioned above.

SPECIES VARIATION

Adult Australian agamid genera belong to 3 size classes: large (total maxillary length - 18-50 mm, total dentary length - 22-50mm); medium (total maxillary length - 11-18mm, total dentary length - 14-20mm); and small (total maxillary length < 11mm, total dentary length < 14mm). Morphometric measurements used herein are illustrated in Fig. 3.

SEXUAL DIMORPHISM

Sexual dimorphism has not been prominent in species studied except for slight size differences. In the *Ctenophorus maculatus* and *C. pictus* species groups, and in *Tympanocryptis intima* pleurodont teeth are larger in the males than in the females, but the overall morphology of the maxilla and acrodont tooth rows are similar.

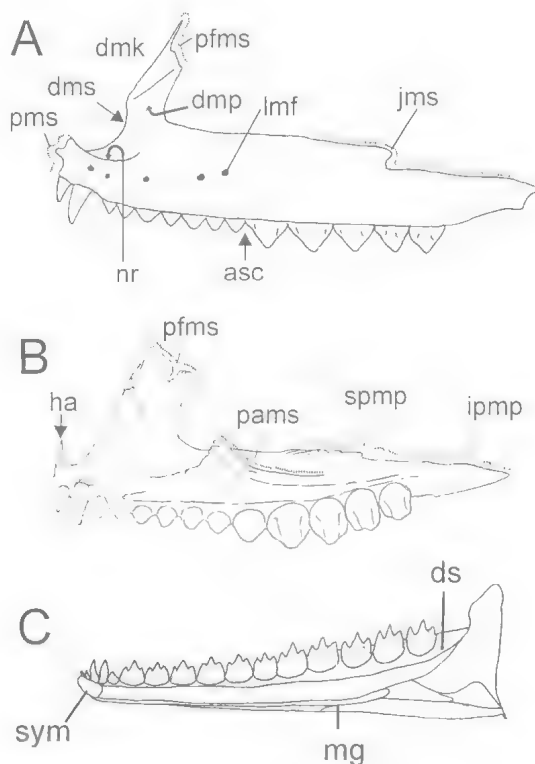


FIG. 4. Morphological features of the agamid maxillae and dentaries. A, B, Maxillary features; C, Dentary features.

SYSTEMATICS

Species not examined in the study are indicated by * in contents lists.

Family AGAMIDAE Gray, 1927

Amphibolurus Wagler, 1830

Amphibolurus is divided into two groups: Group 1 - *A. nobbi* and *A. muricatus*; Group 2 - *A. norrisi*.

Amphibolurus group 1 (Figs 5A-B, 9K)

Species included: *muricatus*, *nobbi nobbi*, *nobbi coggeri*.

Medium-sized.

MAXILLA. Pleurodont teeth 2, medium, unequal sized, closely set, straight, orientated medially; P^1 , $\frac{1}{4}$ - $\frac{3}{4}$ the size of P^2 . 13-14 acrodont teeth in *A. nobbi coggeri*. 16-17 quadrilateral acrodont teeth in *A. nobbi nobbi* and *A. muricatus*. Posteriormost acrodont teeth with antero- and posterocones. Naris ridge residual, only on the

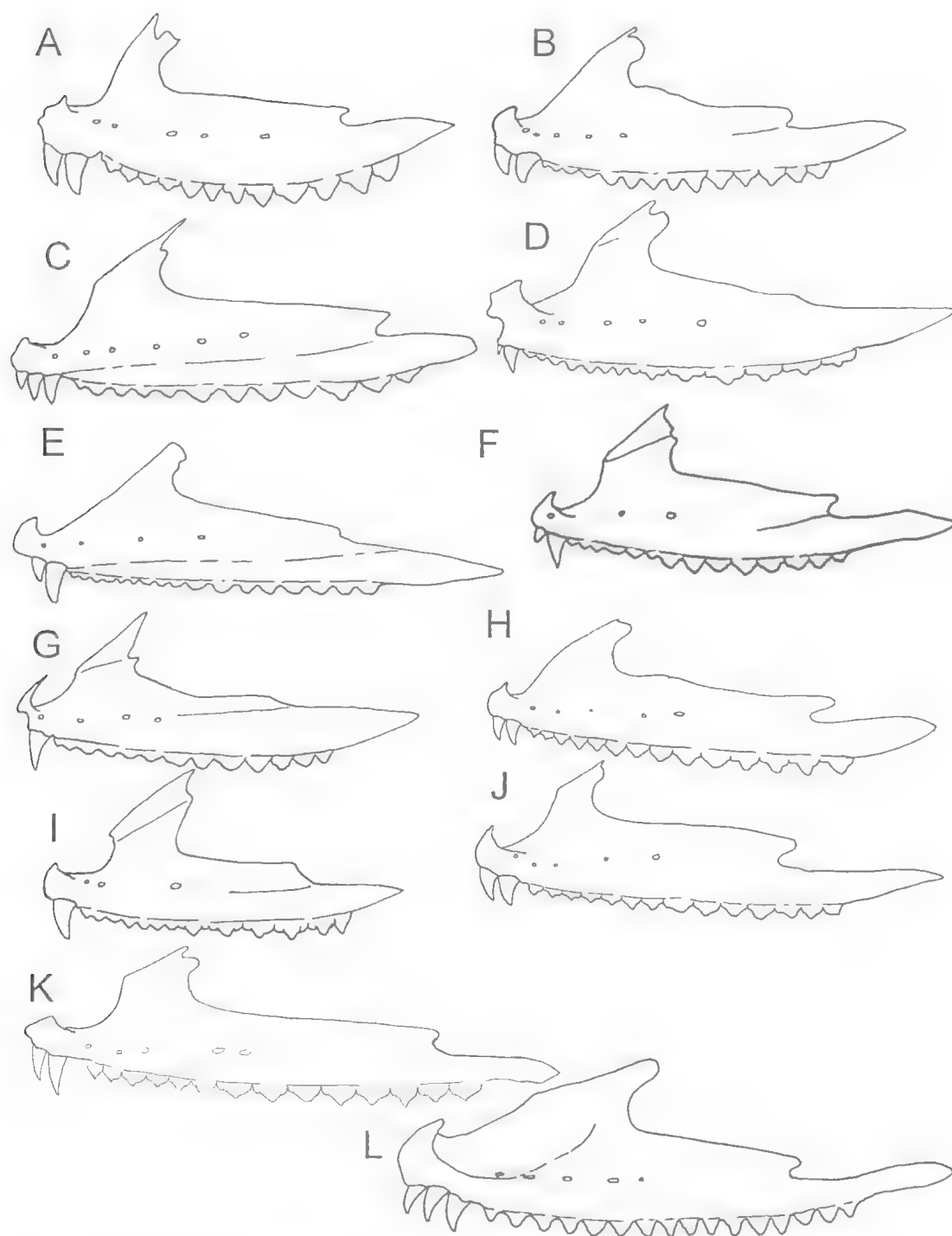


FIG. 5. Maxillae of the Australian agamids in labial view. A, *Amphibolurus muricatus*, x3.85; B, *Amphibolurus nobbi nobbi*, x3.90; C, *Amphibolurus norrisi*, x3.90; D, *Caimanops amphiboluroides*, x4.67; E, *Chlamydosaurus kingii*, x 1.90; F, *Diporiphora bennettii*, x5.63; G, *Diporiphora magna*, x3.76; H, *Lophognathus gilberti gilberti*, x3.3; I, *Diporiphora australis*, x4.0; J, *Lophognathus gilberti centralis*, x3.8; K, *Lophognathus temporalis*, x4.10; L, *Lophognathus longirostris*, x4.0.

anterolateral margin of the narial basin. Dorsal maxillary process slope, angular, approximately 30° from the longitudinal axis of the maxilla. Dorsal maxillary process slope mid-kink indistinct in *A. nobbi nobbi* and *A. muricatus*, yet conspicuous in *A. nobbi coggeri*. Broad dorsal maxillary process between the orbit and external naris. Anterior margin of the maxilla hooked distinctly. A diastema in front of P^1 with a distinct notch between P^1 and the premaxilla. Premaxillary/maxillary suture rounded anteriorly, orientated posterodorsally at its superior end. 3-4 maxillary foramina on labial side. Short and shallow jugal/maxillary suture.

DENTARY. Two, medium, unequally sized, anterolabially orientated pleurodont teeth in *A. nobbi nobbi* and *A. muricatus*. P_1 , $\frac{1}{4}$ the size of P_2 . One caniniform pleurodont tooth in *A. nobbi coggeri*. 16-17 subtriangular acrodon teeth in *A. nobbi nobbi* and *A. muricatus*. 14 subtriangular acrodon teeth in *A. nobbi coggeri*. Anterior end of the dentary narrow, tapering to a small triangular ovoid symphysis. Dentary gracile, long, for its height. 3-4 mental foramina.

REMARKS. *Amphibolurus* shares many features with *Diporiphora*, *Chlamydosaurus*, *Caimanops* and *Lophognathus* including: 1) angular dorsal maxillary process, 2) reduced or no naris ridge, 3) a notch anterior to P^1 and 4) long, gracile dentaries. *Amphibolurus* is distinguished from *Diporiphora* by its much larger size and 2 equally sized maxillary pleurodont teeth, instead of either a singular caniniform pleurodont tooth, or a P^1 , which is much smaller and orientated anterolabially to the P^2 . *A. nobbi coggeri* shares a single large caniniform dentary pleurodont tooth with *Diporiphora*, however, it can be distinguished by being larger and its reduced antero- and posteroconids. *Amphibolurus* is markedly smaller than *Chlamydosaurus* and *Lophognathus* with fewer acrodon teeth and smaller pleurodont teeth. *Amphibolurus* is similar in maxillary length to *Caimanops* but differs by possessing larger, spaced pleurodont, and longer anterior acrodon teeth. *Caimanops* has a more distinct notch anterior of the P^1 . When comparing the ratio of acrodon tooth row length to the number of acrodon teeth, *Amphibolurus* falls within the range of *Lophognathus*, is larger than *Diporiphora* and *Caimanops*, but much smaller than *Chlamydosaurus*.

Amphibolurus group 2 (Fig. 5C)

Species included: *norrissi*

Medium-sized.

MAXILLA. Pleurodont teeth 3, large, recurved, unequally sized, closely spaced, orientated medially, produced labially from the midline of the acrodon tooth arcade. P^1 , $\frac{1}{2}$ the size of $P^{2\&3}$. P^2 equal in size to P^3 . A distinct notch in front of the first pleurodont tooth, producing a short diastema between P^1 the last premaxillary pleurodont tooth. 6-7 maxillary foramina on the labial side. Premaxillary/maxillary suture rounded, orientated posterodorsally at its superior margin. Naris ridge inconspicuous, reduced to the anterior margin of the premaxillary/maxillary suture. Dorsal maxillary process angular, at approximately 30° from the longitudinal axis of the maxilla. Slight kink in the midline of the dorsal maxillary process. Dorsal maxillary process very broad. 13-14 acrodon quadrilateral-shaped teeth. Jugal/maxillary suture long, deep. Maxillary flexure negligible.

DENTARY. Long, gracile, tapering sharply from posterior to anterior. Two, medium-sized, unequal sized, anterolabially orientated pleurodont teeth. P^1 , $\frac{1}{2}$ the size of P^2 . 15-16 simple conical acrodon teeth with reduced antero- and posteroconids. Meckelian groove parallel to dental sulcus in the anterior half of the dentary. Dental sulcus abruptly angled dorsal two-thirds the way down the jaw line. 5-6 mental foramina.

REMARKS. *A. norrisi* has the longest maxillae and dentaries of any *Amphibolurus*, 3 large maxillary pleurodont teeth, reduced antero- and posteroconids. The naris ridge is almost absent, whereas it is only reduced in *A. nobbi* and *A. muricatus*. The dorsal maxillary process is broader in *A. norrisi* than in *A. muricatus* and *A. nobbi*.

Caimanops Storr, 1974 (Fig. 5D)

Species included: *amphiboluroides*

Medium-sized.

MAXILLA. Two, unequal, medially orientated pleurodont teeth with P^1 , $\frac{1}{2}$ the size of P^2 . P^2 recurved. Naris ridge at base of the anterior margin of the narial basin. 4-5 maxillary foramina on the labial side. Dorsal maxillary process slope approximately 45° from the longitudinal axis of the maxilla, with a kink midway up the slope. A distinctly notched diastema between P^1 and the premaxilla. Premaxillary/maxillary suture elaborate,

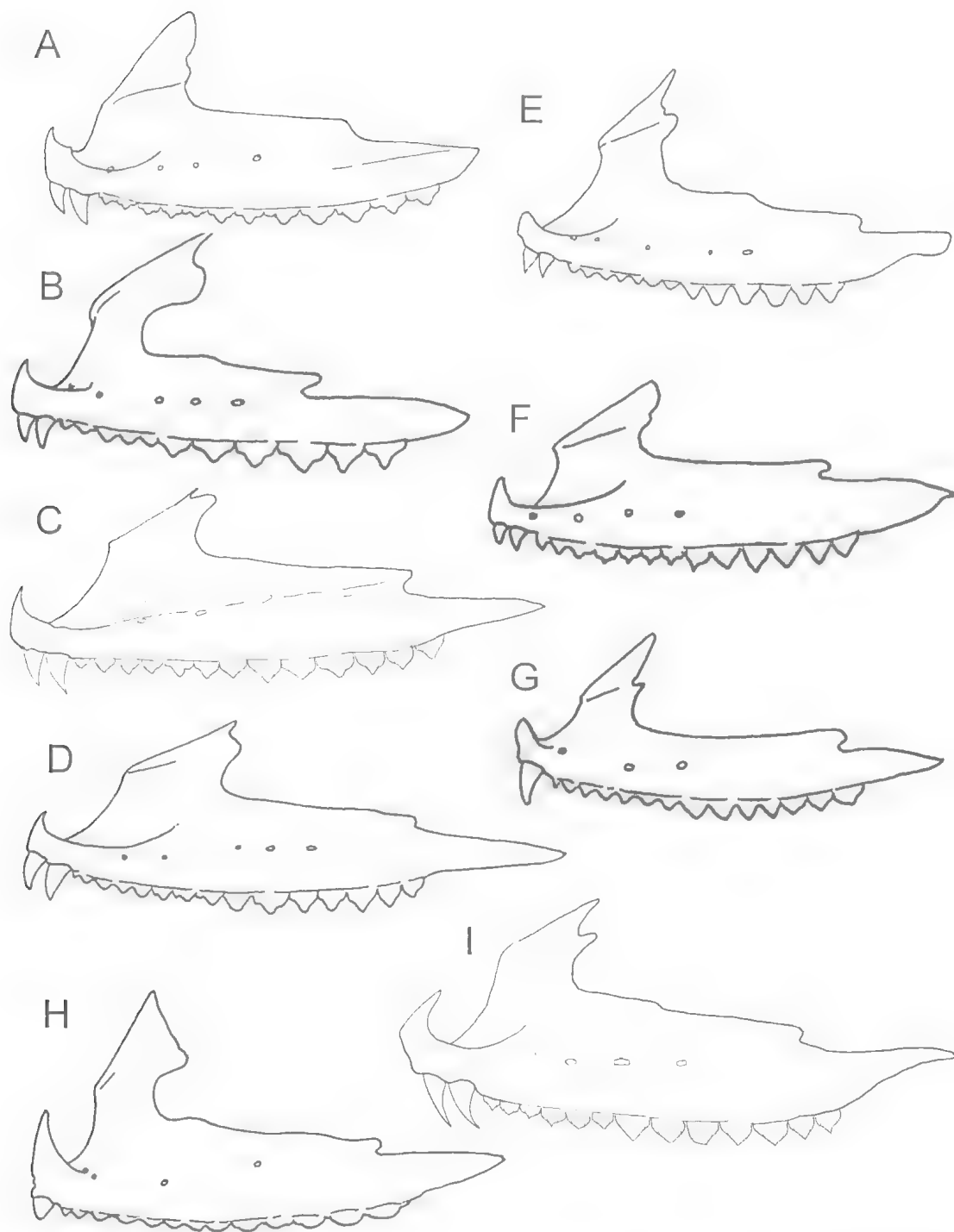


FIG. 6. Maxillae of the Australian agamids in labial view. A, *Ctenophorus caudicinctus*, x5.2; B, *Ctenophorus cristatus*, x4.64; C, *Ctenophorus decresii*, x5.85; D, *Ctenophorus ornatus*, x5.6; E, *Ctenophorus maculatus*, x6.3; F, *Ctenophorus isolepis*, x6.8; G, *Ctenophorus pictus*, x5.54; H, *Ctenophorus nuchalis*, x4.6; I, *Ctenophorus scutulatus*, x4.84.

sigmoid-shaped in lateral profile. Dorsal maxillary process broad. 16 mesocone dominant acrodont teeth with equally sized antero- and posterocones half the size of the mesocone. Jugal/maxillary suture long and shallow.

DENTARY. Two pleurodont teeth with P_1 $\frac{1}{2}$ the size of P_2 . P_2 caniniform. Both pleurodont teeth labially orientated. 17 subtriangular acrodont teeth compressed laterally, of equal size along the dental arcade, broad at their bases. Posteroconid larger than anteroconid. Jaw narrow, tapering abruptly anteriorly. Meckel's groove parallel to the dental sulcus.

REMARKS. *Caimanops* is similar in size to *Amphibolurus*, but has smaller pleurodont and acrodont dentition and a better developed posteroconid. The premaxillary/maxillary notch is also more pronounced in *Caimanops*. *Caimanops* is larger than *Diporiphora* and has smaller pleurodont teeth. *Caimanops* is smaller than *Lophognathus* and is considerably smaller in the pleurodont and acrodont teeth. *Caimanops* is most similar to *Chlamydosaurus*, having an equally prominent premaxillary/maxillary notch, similar pleurodont tooth size difference and general shape of the anterior margin of the maxilla. The second dentary pleurodont tooth of *Caimanops* is large and caniniform, which is markedly similar to the single caniniform dentary pleurodont tooth found in *Chlamydosaurus*. *Caimanops* differs from *Chlamydosaurus* by being much smaller and its more elaborate premaxillary/maxillary suture.

Chelosania Gray, 1845 (Fig. 8D)

Species included: *brunnea*

Medium-sized.

MAXILLA. Pleurodont teeth 1-2, equal, small, similar in size to A^1 , straight, medially orientated. 14-15 acrodont teeth within one dental arcade, with each tooth similar in size along the tooth row. Posteriormost acrodont teeth with distinct postero- and anterocones, anterocones approximately half height of mesocone. Mesocone tip rounded. 5-6 maxillary foramina on the labial side. Naris ridge extending inferior to the narial basin, ending $\frac{3}{4}$ the way up the dorsal maxillary process (near complete). Dorsal maxillary process equally broad along its height, being one of the broadest dorsal maxillary processes for any endemic Australian agamid. Dorsal maxillary process with breadth comparable to *Physignathus*. Dorsal maxillary

process slope steep, at approximately 60° , curving posteriorly at its dorsal margin. Premaxillary/maxillary suture begins immediately in front of P^1 , curving anterodorsally to the premaxilla. This produces a distinctly hooked anterior margin of the maxilla. Jugal/maxillary suture short and deep.

DENTARY. Stout, deep posteriorly. Pleurodont tooth small, medially orientated, equal in size to A^1 . Acrodont teeth 14-15, tricuspid. Postero- and anteroconids equal. Meckel's groove not parallel to the dental sulcus. Subdental bone above the Meckel's groove deep. 3-4 mental foramina.

REMARKS. *Chelosania* bears very few features in common with endemic Australian agamids except *Physignathus lesueurii*, to which it is very similar in many aspects of the skull and jaws. *Chelosania* is also strikingly similar to *Hydrosaurus*, *Physignathus cocincinus* and *Hypsilurus bruynii* from PNG. These features include, a broad dorsal maxillary process and complete naris ridge, which are considered symplesiomorphic. *Chelosania* shares a distinct anteroconid with *Lophognathus gilberti*, *Lophognathus temporalis* and *Caimanops*.

Chlamydosaurus Gray, 1825 (Figs 5E, 9P)

Species included: *kingii*

One of the largest Australian agamids.

MAXILLA. Pleurodont teeth 2, very large, recurved, caniniform, labially orientated, set labially to the acrodont tooth row, with P^2 2-3 times larger than P^1 and recurved labially. A notch in front of P^1 , producing a diastema between the maxilla and the premaxilla. Premaxillary/maxillary suture rounded, angled posteriorly at its dorsal margin, producing a distinctly hooked anterior margin to the maxilla. Naris ridge residual. Dorsal maxillary process slope angled at approximately 45° , with no midline kink. 5-6 maxillary foramina on the labial side of the maxilla. Jugal/maxillary suture long, deep. Broad dorsal maxillary process constricted dorsally. Acrodont teeth 17-18, within a single arcade, of similar size with a single large mesocone.

DENTARY. Long, narrow, tapering sharply posteriorly. Pleurodont tooth large, caniniform, recurved, anterolabially orientated. Acrodont teeth 19-20, conical, monocuspid. Symphysis large, ovoid. Meckel's groove not parallel to the dental sulcus. 4-5 mental foramina.

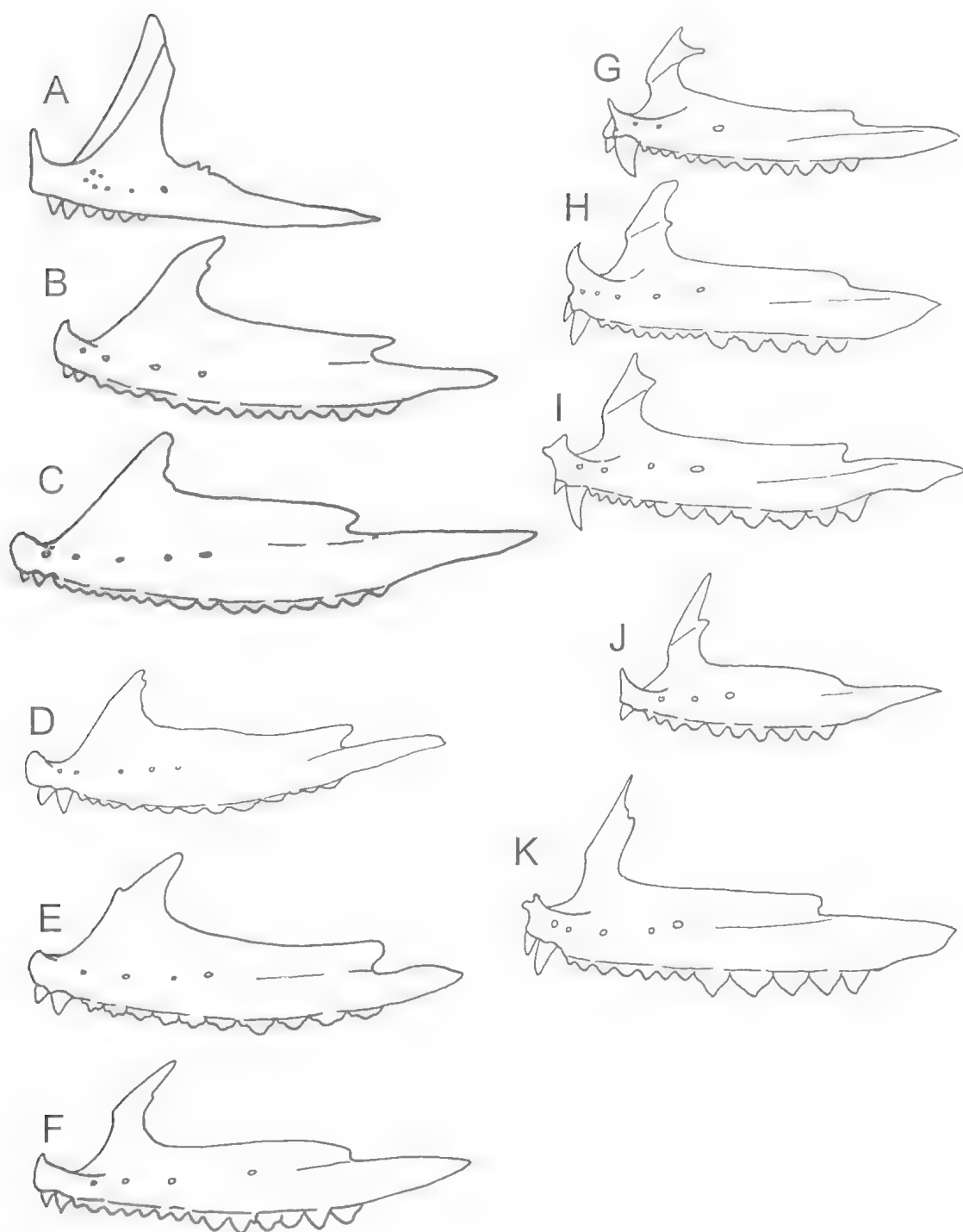


FIG. 7. Maxillae of the Australian agamids in labial view. A, *Moloch horridus*, x5.6; B, *Pogona barbata*, x.55; C, *Pogona vitticeps*, x1.80; D, *Pogona mitchelli*, x2.4; E, *Pogona minor*, x3.15; F, *Rankinia diemensis*, x6.3; G, *Tympanocryptis intima*, x5.2; H, *Tympanocryptis cephalus*, x 5.4; I, *Tympanocryptis tetraporophora*, x6.1; J, *Tympanocryptis parviceps*, x5.1; K, *Tympanocryptis lineata*, x6.2.

REMARKS. *Chlamydosaurus* is the largest of a group comprising *Amphibolurus*, *Diporiphora*, *Caimanops* and *Lophognathus*. It dwarfs all four genera in overall maxillary, dentary and dentition dimensions. It differs from *Amphibolurus* and *Lophognathus* in its unequal maxillary pleurodont teeth and a single caniniform dentary pleurodont tooth. *Chlamydosaurus* differs from *Diporiphora* by its more distinct premaxillary/maxillary notch. *Chlamydosaurus* is most similar to *Caimanops*, from which it only differs significantly in being much larger and having a less complex premaxillary/maxillary suture.

Ctenophorus Fitzinger, 1843

Ctenophorus consists of 8 species groups (Wilson & Knowles, 1988) some of which contain only a single species, but many subspecies. To capture the greatest amount of osteological variation, the present study has taken representatives from all of the species groups used by Wilson & Knowles (1988).

Ctenophorus caudicinctus (Figs 2A, 6A, 9H)

Species included: *caudicinctus*.

Medium-sized; consists of several distinct subspecies (Wilson & Knowles, 1988).

MAXILLA. Pleurodont teeth 2, large, spaced, recurved, unequal, orientated labially. P^1 , $\frac{1}{2}$ the size of P^2 . Naris ridge distinct, bordering the narial basin and up the dorsal maxillary process, half the way. Dorsal maxillary process slope with a distinct kink in the midline. Dorsal maxillary process slope orientated at approximately 45° to the longitudinal axis of the maxilla. Dorsal maxillary process moderately broad. 3-4 maxillary foramina on the labial side, with distinctly hooked anterior end. Acrodon teeth 13-14, mesocone dominant, with small antero- and posterocones. Narial foramen on the dorsal maxillary process. Jugal/maxillary suture short, deep.

Dentary. Pleurodont teeth 2, small, unequal; P_1 small, orientated anterolabially, $\frac{1}{2}$ the size of P_2 . P_2 medium-sized, caniniform, orientated labially. Acrodon teeth 14-15, simple, monocuspid. Mental foramina 3-4.

REMARKS. This species group differs from the *ornatus* species group by its fewer acrodon teeth and a less developed superior process of the posterior margin of the maxilla; from the *decreasii* species group by having spaced maxillary

pleurodon teeth and a better-developed naris ridge; from the *maculatus* species group by its markedly larger maxilla and acrodon tooth; from the *scutulatus* species group by being smaller with fewer acrodon teeth; and from all other species of *Ctenophorus* by its broader and lower dorsal maxillary process, which is not vertical, a better developed naris ridge and a distinct diastema between P^1 of the maxilla and the premaxillary/maxillary suture.

Ctenophorus cristatus (Figs 1D, 6B)

Species included: *cristatus*

Medium-sized. Contains several subspecies.

MAXILLA. Pleurodon teeth 2, medium, equal, recurved, spaced, labially orientated. Premaxillary/maxillary suture curving dorsally, immediately anterior to P^1 , then hooking posterodorsally to the nasals. Narial foramen on the dorsal maxillary process slope. Dorsal maxillary process slope near vertical, with distinct midline kink. A ridge running posterolaterally from this kink to the maxillary/prefrontal suture. Naris ridge moderately developed, bordering the narial basin. Maxillary foramina 4-6, on the labial side. Jugal/maxillary suture deep and long. Superior maxillary process long, producing a tongue-shaped process on the jugal. Acrodon teeth 11-13, mesocone dominant, with small postero- and anterocones.

DENTARY. Pleurodon teeth 2, small, equal, orientated anterolabially. Acrodon teeth 12-14, subtriangular, with simple conical mesoconids and diminutive, equally sized antero- and posteroconids. Meckel's groove parallel to the dental sulcus. Mental foramina 3-4.

REMARKS. *C. cristatus* species group differs from the *pictus* species group by possessing 2 medium-sized, instead of 1 large maxillary pleurodon teeth, by being smaller and having greater ratio of acrodon tooth row length to acrodon tooth count (0.84-0.90 vs. 0.62-0.72).

C. cristatus species group differs from the *reticulatus* species group by possessing a less right-angled dorsal maxillary process relative to the longitudinal axis of the maxilla, larger maxillary and dentary pleurodon teeth and greater ratio of acrodon tooth row length to acrodon tooth count (0.84-0.90 vs. 0.60-0.78).

The *C. cristatus* species group differs considerably from the remaining *Ctenophorus* species groups by its narrower dorsal maxillary

process, higher dorsal maxillary process, smaller maxillary pleurodont teeth, more reduced naris ridge and a more vertically oriented dorsal maxillary process relative to the longitudinal axis of the maxilla.

***Ctenophorus decresii* species group (Fig 6C)**

Species included: *decresii*, *fionni*, *rufescens*.

Medium-sized.

MAXILLA. Pleurodont teeth 1-2, large, closely spaced, recurved, equal, orientated labially. Naris ridge distinct, running the border of the narial basin and up the dorsal maxillary process, half of the way. Dorsal maxillary process with a distinct mid-kink. Dorsal maxillary process slope orientated at approximately 45° to the longitudinal axis of the maxilla. Dorsal maxillary process broadened inferiorly, constricted superiorly. Maxillary foramina 4-5 on the labial side. Distinctly hooked anterior margin with a diastema anterior to P¹. Acrodon teeth 13-14, simple, with small but distinct antero- and posterocones. Narial foramen on the dorsal maxillary process. Jugal/maxillary suture short and deep.

DENTARY. Pleurodont teeth 2, small, unequal; P₁ small, ½ the size of P₂, orientated anterolabially. P₂ medium-sized, caniniform, orientated labially. Acrodon teeth 14-15. Mental foramina 4-5.

REMARKS. The *C. decresii* species group has spaced maxillary pleurodont teeth and a better developed naris ridge than *C. caudicinctus*. *C. decresii* has a deeper subnaris ridge zone and less developed naris ridge than the *C. scutulatus* group. The *C. ornatus* species group is very similar to the *C. decresii* species group differing only in size.

The *C. decresii* differs from the other members of *Ctenophorus* by possessing a broader dorsal maxillary process, better-developed naris ridge, larger pleurodont dentition, by being larger and having less angular dorsal maxillary process in relation to the longitudinal axis of the maxilla. *C. rufescens* is only the second *Ctenophorus* species observed with one large, caniniform maxillary pleurodont tooth. The anterior margin of the maxilla is very similar to other members of the species group, which is in turn considerably different to *C. pictus* – the only other *Ctenophorus* with a single large caniniform pleurodont tooth.

***Ctenophorus ornatus* species group (Fig. 6D)**

Species included: *C. ornatus*, **C. yinnietharra*.

Medium-sized.

MAXILLA. Pleurodont teeth 2, oriented labially, large, spaced, recurved, equal. Naris ridge distinct, running the border of the narial basin and up the dorsal maxillary process slope half of the way. Dorsal maxillary process with a distinct kink in the midline. Dorsal maxillary process slope orientated at approximately 45° from the longitudinal axis of the maxilla. Dorsal maxillary process constricted superiorly, broadening to the inferior margin. Maxillary foramina 4-5, on the labial side. Distinctly hooked anterior margin. Acrodon teeth 12-13, mesocone dominant, with equally sized antero and posterocones. Narial foramen at the base of the dorsal maxillary process. Jugal/maxillary suture short, shallow.

DENTARY. Pleurodont teeth 2, unequal; P₁ small, ½ the size of P₂, orientated anterolabially; P₂ medium-sized, caniniform, orientated labially. Acrodon teeth 14-15, simple, subtriangular. Meckel's groove of uniform depth, parallel to the dental sulcus. Mental foramina 4-5.

REMARKS. The *C. ornatus* species group differs from the *C. scutulatus* species group by possessing a lower dorsal maxillary process and less labial maxillary pleurodont dentition; from the *C. decresii* species group by being smaller; from the *C. caudicinctus* species group by possessing a lower dorsal maxillary process and a less developed superior process of the posterior margin of the maxilla; from the *C. maculatus* species group by its larger maxillary and dentary pleurodont and acrodon teeth its lack of maxillary flexure and its larger size; from the remaining *Ctenophorus* species groups by its broader, lower and less vertical dorsal maxillary process, larger maxillary pleurodont teeth and better developed naris ridge.

***Ctenophorus maculatus* species group (Figs 6E-F, 9E)**

Species included: *maculatus*, *isolepis*, *femoralis*, **fordi*, **rubens*

Small.

MAXILLA. Pleurodont teeth 2, medium-sized, equal, recurved, oriented medially. Diastema between P¹ and premaxilla. Anterior margin of the maxilla distinctly hooked, producing the premaxillary/maxillary suture. Superior margin

of the premaxillary/maxillary suture orientated posterodorsally. Naris ridge borders the narial basin, ending halfway up the dorsal maxillary process. Narial foramen on the dorsal maxillary process slope. Dorsal maxillary process slope oriented near vertical but with a midline kink. Dorsal maxillary process moderately broad relative to maxillary length. Maxillary foramina 3-4, on labial side of the maxilla. Jugal/maxillary suture, long, shallow. Acrodont teeth 12-13, mesocone dominant, with tapered antero- and posterocones. Maxillary flexure present.

Dentary. Pleurodont teeth 2, unequal, anterolabially orientated, with P_1 , $\frac{1}{2}$ the size of P_2 . Acrodont teeth 12-13, subtriangular. Meckel's groove parallel to the dental sulcus. Jaw line elongate, shallow. Mental foramina 3-4.

REMARKS. The *C. maculatus* species group have sexually dimorphic skull. Males in each observed species have larger and more recurved pleurodont dentition than females.

Although much smaller, the *C. maculatus* species group is similar to the *C. ornatus* and *C. caudicinctus* species groups, but it differs from the *C. ornatus* species group by its maxillary flexure, smaller acrodont and pleurodont teeth in the maxilla and dentary and lower ratio of acrodont tooth row length to acrodont tooth count (0.51-0.62 vs 0.77); from the *C. caudicinctus* species group by its smaller and fewer acrodont teeth, less maxillary flexure and lower ratio of acrodont tooth row length to acrodont tooth count (0.51-0.62 vs. 0.60 - 0.74); and from other *Ctenophorus* species groups by its broader dorsal maxillary process, smaller acrodont teeth and distinctly flexed maxilla,

***Ctenophorus pictus* (Figs 6G, 9F)**

Species included: *Ctenophorus pictus*

Medium-sized.

MAXILLA. Pleurodont tooth 1, large, recurved, caniniform, labially orientated. Acrodont teeth 12-13, mesocone dominant, with diminutive antero- and posterocones. Maxillary foramina 4-5. Long and shallow jugal/maxillary suture. Premaxillary/maxillary suture distinct, originating immediately in front of a notch anterior to the pleurodont tooth, orientated anterodorsally. Medially, the suture bends posterodorsally. Dorsal maxillary process slope orientated at greater than 60° to the longitudinal axis of the maxilla, with a midline kink. Dorsal maxillary process broad inferiorly, constricted

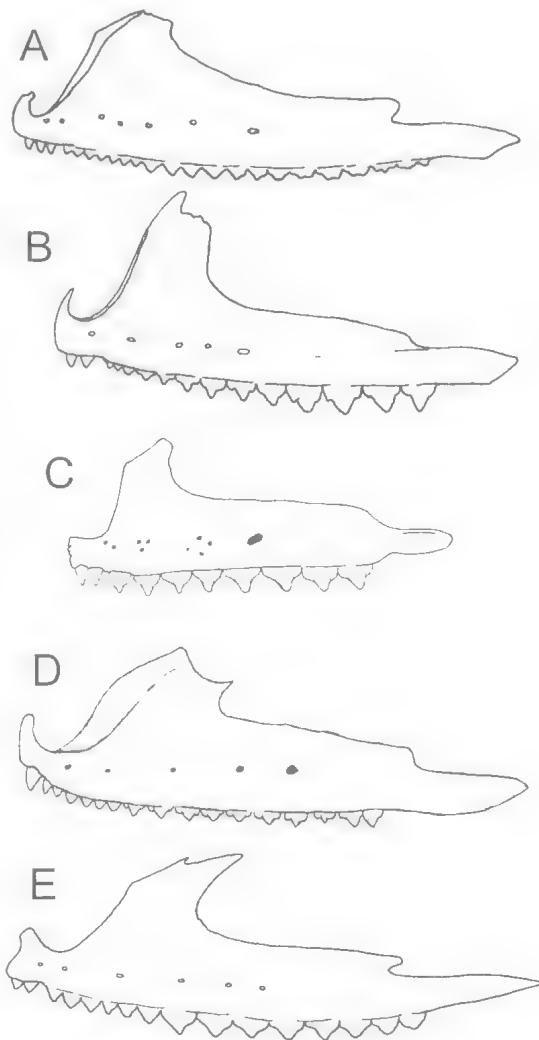


FIG. 8. Maxillae of the Australian agamids in labial view. A, *Physignathus lesueurii*, x1.5; B, *Physignathus lesueurii*, subadult, x2.0; C, *Physignathus lesueurii*, juvenile, x3.8; D, *Chelosania brunea*, x4.2; E, *Hyspilurus spinipes*, x2.8.

superiorly. Naris ridge bordering the narial basin, ending just posterior of this. Superior process of posterior maxillary margin simple, gently curved.

DENTARY. Shallow. Pleurodont tooth 1, large, caniniform, recurved, anterolabially orientated. Acrodont teeth 13-14, subtriangular, laterally compressed. Dental sulcus running parallel to the

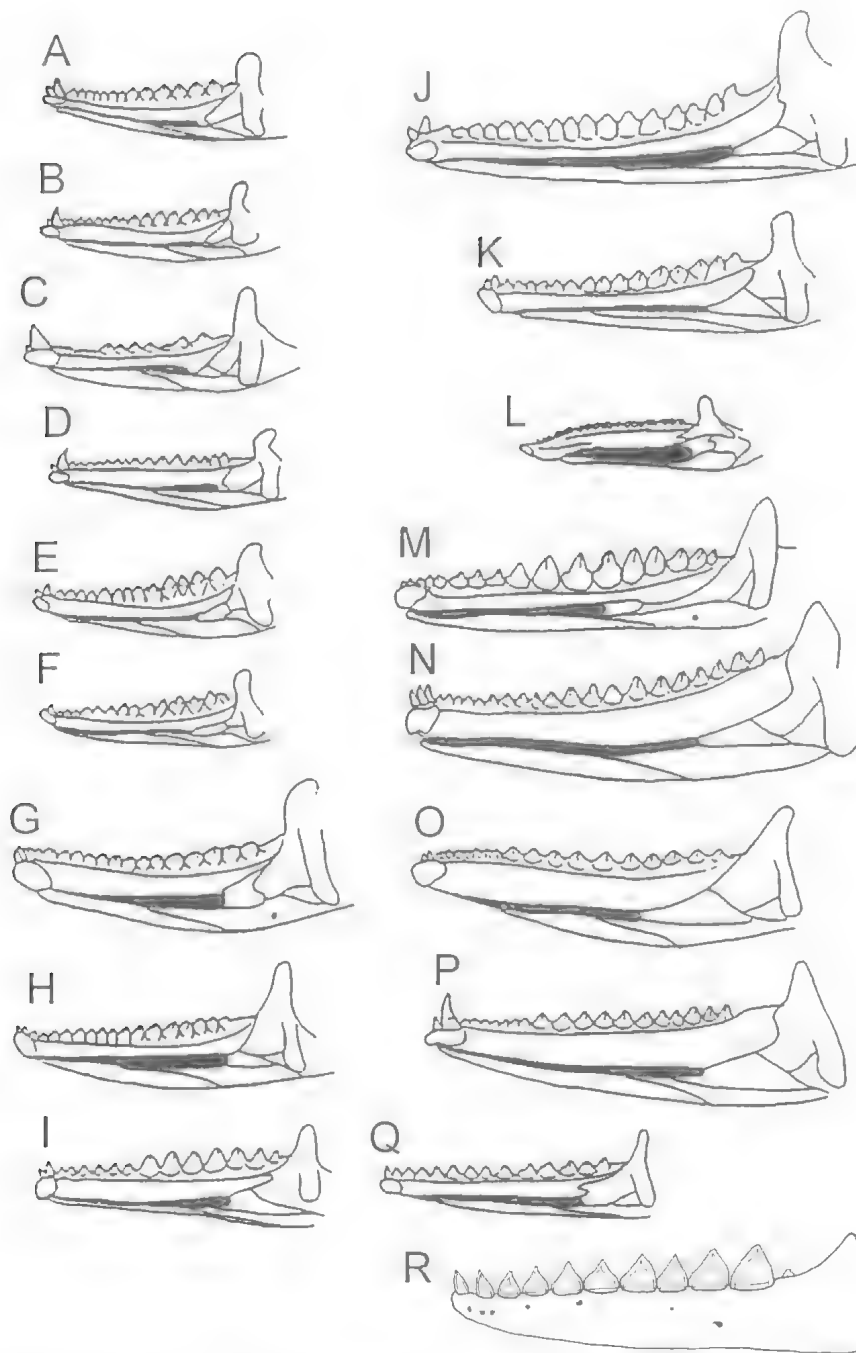


FIG. 9. A selection of Australian agamid dentaries in lingual view. A, *Tympanocryptis lineata*, x2.0; B, *Tympanocryptis cephalus*, x2.0; C, *Tympanocryptis intima*, x2.0; D, *Tympanocryptis tetraporophora*, x2.0; E, *Ctenophorus isolepis*, x2.0; F, *Ctenophorus pictus*, x2.0; G, *Ctenophorus nuchalis*, x2.0; H, *Ctenophorus caudicinctus*, x1.3; I, *Rankinia diemensis*, x3.0; J, *Lophognathus longirostris*, x1.6; K, *Amphibolurus nobbi*, x1.75; L, *Moloch horridus*, x2.0; M, *Hypsilurus spinipes*, x1.5; N, *Physignathus lesueurii*, x1.0; O, *Pogona barbata*, x1.3; P, *Chlamydosaurus kingii*, x1.2; Q, *Diporiphora australis*, x2.0; R, *Physignathus lesueurii*, juvenile, x6.0.

Meckel's groove. Symphysis small, ovoid. Mental foramina 3-4. Narial foramen on the dorsal maxillary process.

REMARKS. This species group exhibits sexual dimorphism with male maxillary and dentary pleurodont teeth being larger and more caniniform than females. It is distinct within the genus by its singular, large, caniniform maxillary and dentary pleurodont dentition. The anterior margin of the maxilla is similar to the *C. cristatus* species group, including the breadth, height and angle of the dorsal maxillary process, development of the naris ridge, and number and size of acrodont teeth.

***Ctenophorus reticulatus* species group**
(Figs 6H, 9G)

Species included: *Ctenophorus reticulatus*, *Ctenophorus nuchalis* and *Ctenophorus maculosus*.

Medium and small-sized.

MAXILLA. Pleurodont teeth 1-2, equal, small, orientated meso-labially, equal to or slightly larger than A^1 . Acrodont teeth 12-15, rounded, labiolingually expanded. Premaxillary/maxillary suture beginning directly anterior to P^1 , with the anterior margin directed vertically to suture with the premaxilla. Naris ridge reduced to border the first portion of the narial basin. Narial foramen on the dorsal maxillary process. Dorsal maxillary process slope near vertical, with reduced or no midline kink. Dorsal maxillary process narrow. Jugal/maxillary suture short, shallow. Maxillary foramina 4-5, on the labial side.

DENTARY. Deep, stout. Pleurodont teeth 1-2, small, equal, labially orientated, same size or slightly larger than A_1 . Acrodont teeth 12-15, rounded, conical in labial profile. Mental foramina 4-5. Meckel's groove broad, not parallel to dental sulcus. Dental sulcus curving dorsally immediately below the last three acrodont teeth.

REMARKS. *C. reticulatus* and *C. nuchalis* are the most similar species. *C. maculosus* differs from *C. reticulatus* and *C. nuchalis* by being smaller, having fewer acrodont teeth, its 2 (not 1) maxillary pleurodont teeth, one large caniniform dentary pleurodont tooth and better developed naris ridge.

The *C. reticulatus* species group differs from the *C. cristatus* species group by its narrower dorsal maxillary process orientated more vertically, smaller maxillary pleurodont teeth, a

less developed naris ridge and a lower ratio of acrodont tooth row length to acrodont tooth count; and from the remaining species of *Ctenophorus* by its narrow dorsal maxillary process, vertically orientated dorsal maxillary process, residual naris ridge and smaller maxillary and dentary pleurodont teeth.

The *C. reticulatus* species group resembles *Pogona* in the narrow dorsal maxillary process, reduced naris ridge, rounded, labiolingually expanded, maxillary and dentary acrodont dentition, small pleurodont teeth equal in size to A^1 and A_1 , but differs in its more vertical dorsal maxillary process, smaller size and smaller acrodont tooth row length to acrodont tooth count ratio.

***Ctenophorus scutulatus* species group**
(Fig. 6I)

Species included: *scutulatus*, **mckenziei*.

Medium-sized. One of largest groups in *Ctenophorus*.

MAXILLA. Pleurodont teeth 2, large, closely spaced, recurved, equal, orientated labially at approximately 20° to the sagittal axis of the maxilla. Naris ridge distinct, running the border of the narial basin and halfway up the dorsal maxillary process slope. Dorsal maxillary process broad, with a distinct kink in the midline. Dorsal maxillary process slope orientated at approximately 45° to the longitudinal axis of the maxilla. Maxillary foramina 5-6, on the labial side. Distinctly vertical and posterodorsal orientation of the premaxillary/maxillary suture. Acrodont teeth 13-14, mesocone dominant, with small tapered antero- and posterocones. Narial foramen on the dorsal maxillary process. Jugal/maxillary suture long, shallow.

DENTARY. Long, gracile. Pleurodont teeth 2, small, unequal; P_1 small, orientated anterolabially, $\frac{1}{4}$ the size of P_2 ; P_2 medium-sized, orientated labially. Acrodont teeth 14-15, subtriangular. Mental foramina 3-4. Symphysis small, ovoid.

REMARKS. The *C. scutulatus* species group does not differ substantially from the *C. decresii* and *C. ornatus* species groups, but differs from all other *Ctenophorus* species by its larger size, better developed naris ridge, broad and angular dorsal maxillary process.

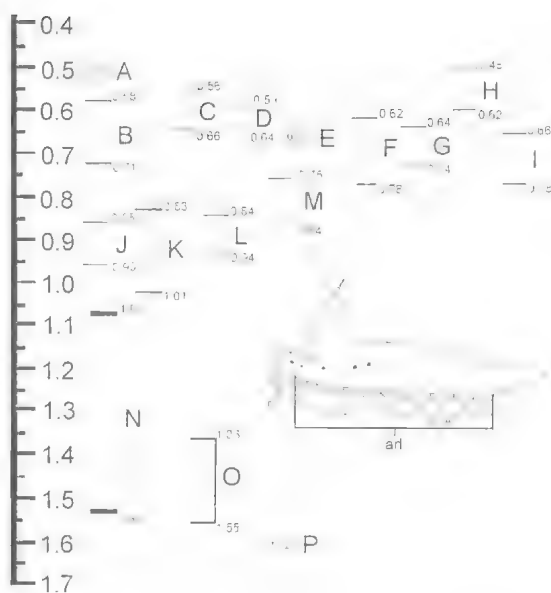


FIG. 10. Maxillary acrodon tooth row length (arl) to acrodon tooth row count for Australian agamid genera. Single figures are mean values for monotypic genera. Range values given for polytypic genera. A, *Moloch*; B, *Diporiphora*; C, *Tympanocryptis*; D, *Rankinia*; E, *Caimanops*; F, *Ctenophorus pictus*; G, *Ctenophorus caudicinctus*; H, *Ctenophorus maculatus* species group; I, *Ctenophorus reticulatus* species group; J, *Amphibolurus*; K, *Lophognathus*; L, *Ctenophorus cristatus*; M, *Ctenophorus decresii* and *Ctenophorus ornatus* species groups combined. N, *Pogona*; O, *Physignathus*; P, *Chlamydosaurus*.

***Diporiphora* Gray, 1842**

Diporiphora is divided into two groups based on the number of maxillary pleurodont teeth. Species not available in this study are *D. convergens*, *D. linga*, *D. reginae* and *D. valens*.

***Diporiphora* group 1 (Fig. 5F)**

Species included: *D. bennettii*, *D. albilabris*.

Medium-sized.

MAXILLA. Pleurodont teeth 2, with $P^1 \frac{1}{2}$ the size of P^2 ; P^2 large, caniniform, recurved, oriented mesolabially. P^1 small, recurved, orientated anteromedially. Acrodon teeth 13-14, monocuspid, subtriangular. Maxillary foramina 3, on the labial side. Naris ridge residual. Dorsal maxillary process low, constricted superiorly, broadened inferiorly. Premaxillary/maxillary suture anterodorsal to P^1 , orientated

posterodorsally. Suture gracile. Acrodon teeth mesocone dominant, with equally sized antero- and posterocones. Jugal/maxillary suture short, relatively deep. Moderate amount of maxillary flex.

DENTARY. Pleurodont teeth 2; P_1 small, orientated anterolabial; P_2 large, caniniform, orientated anterolabially. Acrodon teeth 15-16, subtriangular, with moderately developed posteroconids in the last five teeth. Meckel's groove parallel with the dental sulcus. Symphysis small, ovoid. Mental foramina 5.

REMARKS. Group 1 is the smaller *Diporiphora* species group and differs from group 2 by its 2 maxillary pleurodont teeth, instead of a singular caniniform maxillary pleurodont tooth. *Chlamydosaurus* is the only genus that shares such a massive caniniform dentary pleurodont tooth. *Diporiphora* group 1 differs from *Chlamydosaurus* by being considerably smaller and possessing 4-5 fewer acrodon teeth.

***Diporiphora* group 2 (Figs 2C, 5G, I, 9Q)**

Species included: *D. winneckeii*, *D. magna*, *D. australis*, *D. bilineata*, *D. pindan*

Medium-sized.

MAXILLA. Pleurodont tooth 1, large, recurved, mesolabially orientated, caniniform, labial to the longitudinal maxillary axis. Notch in front of the pleurodont tooth, with the premaxillary/maxillary suture beginning directly above this notch. Suture running dorsally, then reoriented posteriorly. Naris ridge residual. Dorsal maxillary process relatively broad. Dorsal maxillary process slope steep, approximately 60° from the longitudinal axis of the maxilla at its base. Midway up the dorsal maxillary slope it is directed posteriorly at 45° . Acrodon teeth 14-15, mesocone dominant, with little development of antero- or posterocones. Jugal/maxillary suture long, shallow. Maxillary foramina 4.

DENTARY. Pleurodont teeth 2, caniniform, mesolabially orientated, with P_1 very small and P_2 large. Meckel's groove not parallel to the dental sulcus. Symphysis large, ovoid. Acrodon teeth 14, subtriangular, with better developed posteroconid. Mental foramina 4.

REMARKS. Group 2 differs from Group 1 by its singular caniniform maxillary pleurodont tooth.

Lophognathus Gray, 1842

REMARKS. *Lophognathus* is the second largest genus within the group with *Chlamydosaurus*, *Amphibolurus*, *Diporiphora* and *Caimanops*. *Lophognathus*, except *L. longirostris*, is most similar to *Amphibolurus*, but differs in being larger, possessing more prominent maxillary pleurodont teeth, more distinct anterocones, and a broader dorsal maxillary process

Lophognathus group 1 (Figs 1E, 2B, 5H-K)

Species content: *Lophognathus gilberti gilberti*, *L. gilberti centralis*, *L. temporalis*.

Large.

MAXILLA. Pleurodont teeth 2, large, near equal, recurved, closely set, labial to the acrodon tooth row, Naris ridge residual. Dorsal maxillary process slope approximately 45° to the longitudinal axis of the maxilla. Dorsal maxillary process broad, without mid kink. Maxillary foramina 4-5, on the labial side. Premaxillary/maxillary suture rounded, originating directly anterior to P¹. Anterior region including the premaxillary/maxillary suture hooked prominently posterodorsally. Diastema between P¹ and the premaxilla absent. Jugal/maxillary suture long, deep. Acrodon teeth 15, quadrilateral; posterior-most teeth with conspicuous anterocones and sometimes a well-developed posterocone.

DENTARY. Pleurodont teeth 2, labially orientated; P₁ much smaller than P₂, P₂ caniniform, recurved. Symphysis small, ovoid. Acrodon teeth 15-16, antero/mesoconid dominant. Jaw long and gracile in lateral profile. Meckel's groove parallel to the dental sulcus. Mental foramina 3-4.

REMARKS. Group 1 differs from Group 2 by having fewer pleurodont and simpler acrodon teeth.

Lophognathus group 2 (Figs 5L, 9J)

Species included: *Lophognathus longirostris*

This is the largest species of *Lophognathus*.

MAXILLA. Pleurodont teeth 2-3, large, recurved, spaced, set labially away from the acrodon tooth line; P¹ orientated anterolabially, 2/3 the size of P²; P² orientated mesolabially, equal to P³; P³ orientated posterolabially. Naris ridge extending to midway up dorsal maxillary process. Dorsal maxillary process angled

below 45° from the longitudinal axis of the maxilla. Notch anterior to P¹ absent. Premaxillary/maxillary suture rounded, beginning from immediately anterior to P¹. Jugal/maxillary suture short and deep. Maxillary foramina 4-5, on the labial side. Acrodon teeth 16-17, quadrilateral.

DENTARY. Long, narrow. Pleurodont teeth 2-3, unequal, orientated anterolabially; P₁, 1/2 the size of P₂. Where present, P₂ and P₃ are equal. Acrodon teeth 18-19, subtriangular, with no development of the antero- and posteroconids. Meckel's groove parallel to dental sulcus. Symphysis small, ovoid. Mental foramina 4-5

REMARKS. *L. longirostris* is distinct within the genus on its high pleurodont and acrodon tooth count, a broad dorsal maxillary process with a distinct and well-developed naris ridge and its dentary acrodon teeth with indistinct antero- and posteroconids.

Moloch Gray, 1841 (Figs 1F, 2F, 7A, 9L)

Species included: *Moloch horridus*

Small.

MAXILLA. Pleurodont teeth 2-3, equal, small, approximately equal to A¹. Acrodon teeth 15, orientated lingually at approximately 80° to the longitudinal axis of the maxilla, triangular, with a single mesocone, without antero- and posterocones, wear produces the crowns into a sculptured crescentic shape. Naris ridge complete, running the length of the dorsal maxillary process. A diastema between P¹ and the premaxilla. Premaxillary/maxillary suture curved anterodorsally, produced by a thin anterior spike of the maxilla. Jugal/maxillary suture without a superior posterior maxillary process, therefore has no distinguishable depth, long, running from the palatine/maxillary suture to the posterior margin of the posterior maxillary process. Dorsal maxillary process near vertical, narrow in lateral view, broad in anterior view, expanded laterally to be a broad partition between orbit and naris. Labial maxillary foramina 6-7.

DENTARY. Pleurodont teeth 2-3, small, equal, spaced, similar in size to A₁. Acrodon teeth 15-16, with antero- and posteroconids orientated dorsoventrally along the longitudinal axis, with mesoconid orientated labiolingually to the longitudinal line, with anteroeristid developed into a posterolabially directed lophid, with

ostero Cristid developed into an anterolabially directed lophid. Meckel's groove very wide, with a heavily reduced dental sulcus. Symphysis tiny, oval. Mental foramina 5-6.

REMARKS. This taxon shares no close maxillary or dentary characters with any other Australian agamid. Although *Moloch* is highly derived for a small-sized dragon, it has a near complete naris ridge, high maxillary foramina count and a high maxillary pleurodont count.

Physignathus Cuvier, 1829
(Figs 1A, 8A-C, 9N, R)

Species included: *Physignathus lesueurii*, *Physignathus cocincinus*.

Large.

MAXILLA. Pleurodont teeth 3, medium-sized, equal, labially orientated, straight. Premaxillary/maxillary suture beginning directly anterior to the first pleurodont tooth, producing a hooked anterior margin of the maxilla. Dorsal maxillary process broad. Naris ridge complete, originating near the premaxillary/maxillary suture, terminating beneath the nasal bone, anterior to the maxillary/prefrontal suture. Narial basin deep. Maxillary foramina 6-7, on labial side. Jugal/maxillary suture short, deep. Acrodon teeth 18-19, quadrilateral, with well-developed equal antero and posterocones half the size of the mesocone. Dorsal maxillary process slope steep, approximately 60° from the longitudinal axis of the maxilla.

DENTARY. Deep, stout. Pleurodont teeth 3, medium-sized, equal, orientated anterolabially. Acrodon teeth 18, with a slightly developed anteroconid. Meckel's groove broad, beginning anterior to the last 4-5 acrodon teeth. Mental foramina 5-6.

REMARKS. *Physignathus* shares with *Chelosania* a distinct naris ridge, broad dorsal maxillary process, and a deep, stout dentary, but differs by being much larger and possessing a greater number of pleurodont and acrodon teeth.

Pogona Storr, 1982
(Figs 1G-H, 2E, 7B-E, 9O)

Species content: *barbata*, *vitticeps*, *minor*, *mitchelli*, *nullabor*, **henrylawsoni*.

Pogona is a medium-sized to large-sized agamid genus. *Pogona henrylawsoni* is the smallest of

the group, however, it was not available for this study.

MAXILLA. Pleurodont teeth 2, small to medium-sized, unequal in small species (*minor*, *mitchelli*, *nullabor*) with P¹ orientated anterolabially to P², equal in large species (*vitticeps*, *barbata*) with P^{1&2} approximately the same size or slightly larger than A¹. Acrodon teeth 11-17, rounded, with conspicuously rounded cones. Maxillary foramina 3-4, on the labial side. Mesocone expanded labiolingually. Dorsal maxillary process steep, approximately 60° from the longitudinal axis of the acrodon tooth row, narrow superiorly, broad basally. Jugal/maxillary suture long, deep. Naris ridge residual. Premaxillary/maxillary suture rounded, continuous with the premaxilla. Anterior margin of the maxilla hooked slightly.

DENTARY. Stout, robust, deep in larger species. Pleurodont teeth 2, small to medium-sized; in large species small, equal, similar in size to A¹; in small species medium-sized, orientated anterolabially for P₁ and mesolabially for P₂. P₁, ½ the size of P₂. Acrodon teeth 13-20, rounded, conical in lateral profile. Mental foramina 4-5.

REMARKS. *Pogona* shares with the *Ctenophorus reticulatus* species group a high and near vertical dorsal maxillary process, rounded acrodon dentition, deep posterior margin of the dentary and small equally sized pleurodont teeth (in the larger species) but differs by being much larger (with the possible exception of *Pog. henrylawsoni*), having broader dorsal maxillary processes inferiorly, larger and more acrodon teeth and greater acrodon tooth length to acrodon tooth number ratio (1.06-1.53 vs. 0.6-0.78).

Rankinia Wells & Wellington, 1985
(Figs 7F, 9I)

Species included: *R. diemensis*, *R. adelaidensis*, *R. chapmani*

Small.

MAXILLA. Pleurodont teeth 2-3, small, equal, closely set, orientated meso-labially. Acrodon teeth 11-13, subtriangular, with distinct, equally sized antero- and posterocones. Mesocone very large, at least twice the size of the antero- and posterocones. Naris ridge reduced. Dorsal maxillary process narrow, near vertical. Premaxillary/maxillary suture rounded, continuous with the line of the pleurodont teeth.

A small diastema occurs directly anterior to P^1 . Maxillary foramina 3-5. Jugal maxillary suture long, shallow. Narial foramen at the base of the dorsal maxillary process.

DENTARY. Long, gracile, with rounded anterior, with very small symphysis. Pleurodont teeth 2, small, spaced, equal, straight, mesolabially orientated. Acrodont teeth 14, subtriangular, with reduced antero- and posterocones. Mental foramina 4-5.

REMARKS. *Rankinia* is most similar to *Tympanocryptis* and the *Ctenophorus reticulatus* species group with its constricted, near vertical dorsal maxillary process, reduced naris ridge and small size, but it differs from the *C. reticulatus* species group by having shallower maxillae and dentaries and from *Tympanocryptis* by the lack of caniniform pleurodont teeth in both the maxilla and dentary.

***Tympanocryptis* Peters, 1863**
(Figs 7G-K, 9A-D)

Species included: *intima*, *cephalus*, "*lineata*", *tetraporophora*, *parviceps*, **uniformis*.

Small.

MAXILLA. Pleurodont teeth 2; P^2 caniniform, oriented mesolabially, twice the size of P^1 ; P^1 oriented either anterolabial (*tetraporophora*, *intima*) or mesolabial ("*lineata*", *cephalus*). Acrodont teeth 12-13, mesocone dominant, with equal antero- and posterocones. Premaxillary/maxillary suture directly anterodorsal of the pleurodont teeth, high above the tooth row with a distinct mid-length notch, continuing dorsally, produced by the hooked anterior margin of the maxilla. Dorsal maxillary process narrow. Naris ridge reduced to border the length of the narial basin. Dorsal maxillary process slope near vertical. Foramina 3-5, on the labial side. Jugal/maxillary suture long, beginning above the last 4-5 acrodont teeth.

DENTARY. Short, stout. Pleurodont teeth 2, closely spaced, anterolabially orientated; P^1 $\frac{1}{2}$ the size of P^2 ; P^2 large, caniniform. Acrodont teeth 13-14, subtriangular, with indistinct antero- and posteroconids. Dental sulcus narrow, running the entire length of the dentary. Meckel's groove parallel to dental sulcus. Meckelian groove narrowed anteriorly, sometimes closed in *T. intima*. Mental foramina 2-3.

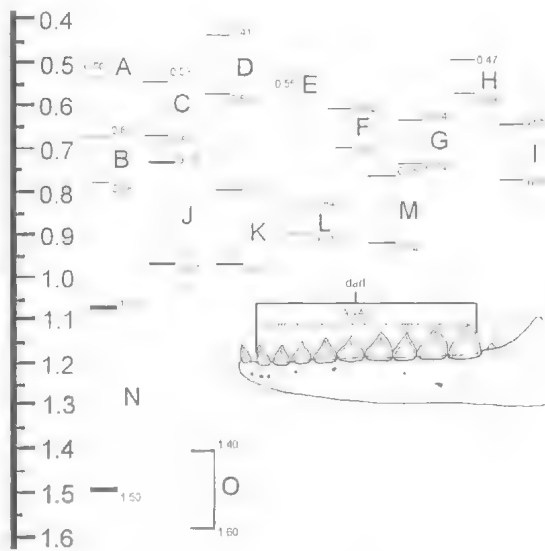


FIG. 11. Dentary acrodont tooth row length (darl) to acrodont tooth row count for Australian agamid genera. Single figures are mean values for monotypic genera. Range values given for polytypic genera. A, *Moloch*; B, *Diporiphora*; C, *Tympanocryptis*; D, *Rankinia*; E, *Caimanops*; F, *Ctenophorus pictus*; G, *Ctenophorus caudicinctus*; H, *Ctenophorus maculatus* species group; I, *Ctenophorus reticulatus* species group; J, *Amphibolurus*; K, *Lophognathus*; L, *Ctenophorus cristatus*; M, *Ctenophorus decresii* and *Ctenophorus ornatus* species groups combined; N, *Pogona*; O, *Physignathus*; P, *Chlamydosaurus*.

REMARKS. *Tympanocryptis* is easily distinguished from all other Australian agamids by the shape of the anterior maxillary margin, shape of the premaxillary/maxillary suture, very large caniniform P^2 on both maxillary and dentary and constricted, near vertical dorsal maxillary process.

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LITERATURE CITED

- ARCHER, M. 1978. Quaternary vertebrate faunas from the Texas Caves of southeastern Queensland. *Memoirs of the Queensland Museum* 19: 61-109.
- BADHAM, J.A. 1976. The *Amphibolurus barbatus* species group (Lacertilia: Agamidae). *Australian Journal of Zoology* 24: 423-443.
- COGGER, H.G. 2000. Reptiles and amphibians of Australia 5th ed. (Reed: Melbourne) 796p.
- 1961 An investigation of the Australian members of the family Agamidae (Lacertilia) and their phylogenetic relationships. Unpublished MSc thesis, University of Sydney.
- COOPER, J.S., POOLE, D.F.G. & LAWSON, R. 1970. The dentition of agamid lizards with special reference to tooth replacement. *Journal of Zoology (London)* 162: 85-98.
- COVACEVICH, J., COUPER, P., MOLNAR, R.E., WITTEN, G. & YOUNG, W. 1990. Miocene dragons from Riversleigh: new data on the history of the family Agamidae (Reptilia: Squamata) in Australia. *Memoirs of the Queensland Museum* 29: 339-360.
- ESTES, R. 1983 The fossil record and early distribution of lizards. Pp 365-398. In Rhodin, A. & Miyata, K. (eds) *Advances in herpetology and evolutionary biology: essays in honor of Ernest E. Williams*. (Museum of Comparative Zoology, Harvard University: Cambridge, Mass).
- FROST, D.R. & ETHERIDGE, R. 1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). University of Kansas, Museum of Natural History Miscellaneous Publications 81: 1-65.
- GREER, A.E. 1987. Observations on the osteology and the natural history of the agamid lizard *Ctenophorus clayi*. *Western Australian Naturalist* 17: 5-7.
- 1989a Observations on the osteology and natural history of the agamid lizard *Ctenophorus femoralis*. *Western Australian Naturalist* 18(1): 21-23.
- 1989b. The biology and evolution of Australian lizards. (Surrey Beatty & Sons: Chipping Norton, NSW) 264p.
- KENT, D.S. 1987. Notes on the biology and osteology of *Amphibolurus diemensis* (Gray, 1841), the mountain dragon. *Victorian Naturalist* 104: 101-104.
- LYDEKKER, R. 1888. Catalogue of fossil reptilia and amphibia in the British Museum (Natural History) Part I. 276p.
- MACKNESS, B.S. & HUTCHINSON, M.N. 2000. Fossil lizards from the early Pliocene Bluff Downs Local Fauna. *Transactions of the Royal Society of South Australia* 124: 17-30.
- MITCHELL, F.J. 1965 The affinities of *Tympanocryptis maculosa* Mitchell (Lacertilia-Agamidae). *Records of the South Australian Museum* 15: 179-191.
- MOLNAR, R.E. & KURZ, C. 1997. The distribution of Pleistocene vertebrates on the eastern Darling Downs, based on the Queensland Museum collections. *Proceedings of the Linnean Society of New South Wales* 117: 107-134.
- MOLNAR, R.E. 1991. Fossil reptiles in Australia. Pp 605-702. In Vickers-Rich, P., Monaghan, J.M., Baird, R.F. & Rich, T.H. (eds) *Vertebrate palaeontology of Australasia*. (Pioneer Design Studio: Melbourne).
- MOODY, S. M. 1980. Phylogenetic and historical biogeographical relationships of the genera in the family Agamidae (Reptilia: Lacertilia). Unpublished Ph.D. Thesis, University of Michigan, Ann Arbor.
- SMITH, M.J. 1976. Small fossil vertebrates from Victoria Cave, Naracoorte, South Australia IV. Reptiles. *Transactions of the Royal Society of South Australia* 100(1), 39-51.
- SMITH, W.J.S., OSBORNE, W.S., DONNELLAN, S. & COOPER, P.D. 1999. The systematic status of earless dragon lizards, *Tympanocryptis* (Reptilia: Agamidae), in south-eastern Australia. *Australian Journal of Zoology* 47, 551-564.
- WILSON, S.K. & KNOWLES, D.G. 1988. Australia's reptiles. A photographic reference to the terrestrial reptiles of Australia. (Collins: Sydney).
- WITTEN, G.J. 1982. Comparative morphology and karyology of the Australian members of the family Agamidae and their phylogenetic implications. Unpublished Ph.D. Thesis, Department of Anatomy, University of Sydney, 272 pp.
1993. Family Agamidae. Pp. 240-252 In Glasby, C.J., Ross, G.J.B. & Beesley, P.L. (eds) *Fauna of Australia, Vol 2A Amphibians and Reptiles* (Australian Government Printing Service: Canberra).

APPENDIX 1

SKULL COMPARATIVE MATERIAL LIST

Agama stellio; MNHN1991.4020, *Amphibolurus muricatus*; QMJ1042, AMR-unregistered, AMR1480, *Amphibolurus nobbi nobbi*; QMJ38748, *Amphibolurus nobbi coggeri*; SAMR13162, *Amphibolurus norrisii*; WAMR unregistered, *Caimanops amphiboluroides*; WAMR14464, *Calotes citellatus*; MNHN 1991.4002, *Chelosania brunnea*;

NTR8700, NTR9924, *Chlamydosaurus kingii*; QMJ3718, QMJ5707, QMJ19707, QMJ21929, QMJ47642, *Ctenophorus caudicinctus*; QMJ21654, SAMR03467, SAMR29492, WAMR82712, WAMR47832, WAMR47833, NTR1557, NTR11115, *Ctenophorus clayi*; WAMR71343, *Ctenophorus cristatus*; SAMR3026, SAMR3029, SAMR20771, WAMR47841, WAMR101474, NTR1096,

NTR9208, *Ctenophorus decrevii*; AMR81641, SAMR9382, SAMR9385, NTR6956, *Ctenophorus femoralis*; WAMR47835, *Ctenophorus fionii*; QMJ274, SAMR9230, SAMR10105, SAMR13320, SAMR13899, NTR8263, *Ctenophorus jordi*; QMJ50835, QMJ22734, *Ctenophorus isolepis* (juvenile) QMJ48488, QMJ24824, SAMR5303, SAMR15517B, SAMR15517F, NTR20437, NTR31418, *Ctenophorus maculatus*; WAMR14021, *Ctenophorus maculosus*; SAMR unregistered X 2, *Ctenophorus nichalis*; QMJ705, SAMR7304, SAMR7309, WAMR28140, WAMR47837, WAMR82656, WAMR13073, NTR18496, NTR18819, NTR31417, NTR31418, *Ctenophorus ornatus*; WAMR30073, *Ctenophorus pictus*; QMJ48074, SAMR741, SAMR8952, SAMR14479, SAMR19249, SAMR26561, WAMR66973, NTR17428, NTR18497, *Ctenophorus reticulatus*; SAMR29252, WAMR47834, 93129, *Diporiphora albilabris*; NTR1232, NTR4101, *Diporiphora australis*; QMJ44926, QMJ29907, *Diporiphora bennetti*; NTR9490, NTR32541, *Diporiphora bilineata*; QMJ11141, QMJ44926, *Diporiphora lalliae*; NTR286, NTR1514, *Diporiphora magna*; NTR3685, NTR22619, *Diporiphora winnicketi*; NTR11133, NTR15099, *Gonocephalus grandis*; WAMR49516, UMMZR170383, *Hydrosaurus pustulatus*; UMMZR188050, UMMZR188058, *Hypsilurus bowdii*;

QMJ17799, QMJ1002, *Hypsilurus spinipes*; QMJ8330, QMJ42424, QMJ45306, *Lophognathus gilberti*; QMJ39042, NTR33496, NTR33499, *Lophognathus longirostris*; QMJ61729, NTR15248, NTR33570, NTR10867, *Lophognathus temporalis*; QMJ46374, NTR6184, NTR22947, *Moloch horridus*; QMJ11492, SAMR22514, *Physignathus cocincinus*; MNHN1991.4259-60, *Physignathus lesuerii*; QMJ5449, QMJ26671, QMJ38108, QMJ43834, QMJ47973, *Pogona barbata*; QMJ14402, QMJ23950, QMJ47070, QMJ47077, QMJ57296, *Pogona minor*; NTR31429, SAMR587, SAMR14857, *Pogona mitchelli*; NTR10576, NTR31430, *Pogona nullabor*, SAMR18581,

Pogona vitticeps; QMJ37168, QMJ37167, *Rankinia adelaidensis*; WAMR9831, *Rankinia diemenensis*; AMR70141, WAMR9830, *Tympanocryptis cephalus*; QMJ21659, NTR16767, NTR16768, *Tympanocryptis intima*; QMJ47889, SAMR14422, SAMR15323, *Tympanocryptis lineata*; QMJ8604, NTR18746, NTR23209, *Tympanocryptis tetraporophora*; QMJ34580, SAMR16599, *Uromastix acanthinura*; MNHN 1991.4265-57.

APPENDIX 2

Key to modern Australian agamid genera using the maxilla.

1. Naris ridge present 2
Naris ridge absent, or residual 3
2. Naris ridge complete (or near complete) 4
Naris ridge ends posterior to the narial basin, on the dorsal maxillary process 5
Naris ridge borders narial basin 6
3. Dorsal maxillary process broad *Hypsilurus*
Dorsal maxillary process constricted superiorly and broad inferiorly 7
4. One pleurodont tooth and a broad dorsal maxillary process *Chelosania*
Two or usually three pleurodont teeth 8
5. One, large, caniniform pleurodont tooth *Ctenophorus pictus* or *Ctenophorus rufescens*
Two, equal, large, pleurodont teeth *Ctenophorus ornatus*, *Ctenophorus decrevii*, *Ctenophorus caudicinctus* and *Ctenophorus scutulatus* sp. groups.
Two, equal small, to medium-sized pleurodont teeth *Ctenophorus maculatus* sp. group
Three, spaced, recurved pleurodont teeth *Lophognathus longirostris*
6. Two, equal pleurodont teeth 9
Two, unequally sized pleurodont teeth with the second caniniform, with a distinct notch anterodorsal to P1 *Tympanocryptis*
7. One, large, caniniform tooth *Diporiphora* sp. group 1
Two, P¹ at least twice the size of P² 10

- Two, P¹ approximately 2.4 or equal to P² 12
- Three large pleurodont teeth *Amphibolurus norrisi*
8. Aerodont teeth orientated parallel to the longitudinal axis of the maxilla *Physignathus*
Aerodont teeth orientated lingually at approximately 90° from vertical axis of maxilla *Moloch*
9. Narial foramen on dorsal maxillary process 11
Narial foramen within narial basin. Very long narial maxillary suture *Rankinia*
10. Premaxillary/maxillary suture distinctly ornate, sigmoid-shaped. Total maxillary length less than 18mm *Caimanops*
Premaxillary/maxillary suture simple, rounded suture. Total maxillary length greater than 30mm *Chlamydosaurus*
Premaxillary/maxillary suture simple, rounded suture. Total maxillary length less than 15mm *Diporiphora* group 2
11. Aerodont teeth with rounded crowns, with equally sized antero- and posterocones *Ctenophorus reticulatus* species group
Aerodont teeth with mesocone dominant, with tooth crowns not distinctly rounded *Ctenophorus cristatus*
12. Aerodont teeth quadrilateral 13
Aerodont teeth with rounded crowns, with equally sized antero- and posterocones *Pogona* (only applicable if dentary dentition is known)
13. Anteroconid distinct, posteroconid reduced or absent *Lophognathus*
Both antero- and posteroconids reduced *Amphibolurus nobbi*; *A. muricatus*.

MORPHOMETRIC AND REPRODUCTIVE NOTES ON THE RARE WET TROPICS SKINK, *GLAPHYROMORPHUS MJOBERGI*. *Memoirs of the Queensland Museum* 48(1): 146. 2002:- *Glaphyromorphus mjobergi* (Lönnerberg & Andersson, 1915) is a rare skink (Cogger et al. 1993), confined to rainforest above 650m in Queensland's Wet Tropical Coast Biogeographical Region. Thirtysix individuals are held in the Australian, Queensland and Field Museums.

The major part of the known range of *G. mjobergi* is on the Atherton and Evelyn Tablelands (Covacevich & McDonald, 1993) where rainforests have been fragmented by >100 years of clearing (Winter et al., 1987). Between November 1995 and January 2000, 8 surveys were undertaken in these fragments and 8 continuous forest sites were searched to assess the effect of rainforest fragmentation on reptiles. Animals were hand-caught, measured, sexed and released at point of capture (Sumner et al., 1999).

Forty-seven *Glaphyromorphus mjobergi* were captured at 6 sites, 3 in continuous forest and 3 in rainforest fragments. All were found in rotting logs on the rainforest floor. Field identifications were based on extremely short limbs relative to body length and orange flush over the forelimbs (Cogger, 2000). Greatest numbers were captured at a continuous forest site at Massey Creek (Table 1); 22 individuals were captured over 7 surveys. The 3 rainforest fragments in which *G. mjobergi* was captured were very small; Maalan Road is ~2.5 hectares, and the Woolward property fragments are both <1 hectare.

SVL was 36-97mm (av. 70) (Table 1). Total length (TL) was 42-248mm (av. 168). Twelve of 39 individuals caught possessed their original tails, regenerated tails being easily recognized by colour and pattern changes below the abscission point. For individuals with original tails TL was 91-231mm (av. 176). Individuals weighed 6.4-17g (av. 12.4).

Of the 3 gravid females captured 2 had at least 4 eggs visible in the abdomen, and SVLs of 80, 85 and 97mm and TLs of 228, 200 and 197mm, respectively (only the first individual retained its original tail). Eversion of hemipenes identifies male reptiles, however this proved difficult due to the hard, slippery nature of the scales in this species. Two individuals verified as male using this method had SVLs of 80 and 69mm and TLs of 165 and 182mm, respectively. Neither

retained its original tail.

Of 13 sites surveyed at which *G. mjobergi* was absent, all but one was to the northeast of the sites where *G. mjobergi* was present. This pattern suggests very specific habitat requirements, perhaps related to rainfall. The fact that half the sites at which *G. mjobergi* were recorded are rainforest fragments suggests that this species is reasonably robust to the effects of anthropogenic fragmentation. Fewer individuals were captured on average in fragments ($X = 5$) compared to continuous forest sites ($X = 10.7$), however differences in site size and search effort confound any comparison. Designation of this species as 'rare' is appropriate due to its restricted distribution. However, it appears more common than has been estimated from museum records (Cogger et al. 1993).

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Literature Cited

- COGGER, H.G. 2000. Reptiles and amphibians of Australia. (Reed: Sydney).
- COGGER, H.G., CAMERON, E.E., SADLER, R.A., EGGLE, P. 1993. The action plan for Australian reptiles. (Australian Nature Conservation Agency).
- COVACEVICH, J.A. & McDONALD, K.R. 1993. Distribution and conservation of frogs and reptiles of Queensland rainforests. *Memoirs of the Queensland Museum* 34(1): 189-199.
- FRANKEL, O.H. & SOULE, M.E. 1981. Conservation and Evolution. (Cambridge University Press: Cambridge).
- SUMNER, J., MORITZ, C., & SHINE, R. 1999. Shrinking forest shrinks skink: morphological change in response to rainforest fragmentation in the prickly forest skink (*Gnypetoscincus queenslandiae*). *Biological Conservation* 91: 159-167.
- WINTER, J.W., BELL, F.C., PAHL, L.I., & ATHERTON, G.G. 1987. Rainforest clearfelling in northeastern Australia. *Proceedings of the Royal Society of Queensland* 98: 41-57.

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TABLE 1. Locality (Longitude: Long. and Latitude: Lat.), number of individuals (No. caught) and morphological measurements of *Glaphyromorphus mjobergi* caught at each site. Morphological measurements included snout to vent length (SVL), total length (Total L) interlimb length (Interlimb L), weight, head length (Head L) and head width (Head W). Measurements for individuals at 'Reynolds' were available for only one individual.

Site	Long.	Lat.	No caught		SVL	Total L	Interlimb L	Weight	Head L	Head W
Maalan Road	145° 34'	17° 44'	13	Min	36	65	21	8.1	4.9	4.7
				Max	88	228	53	14	15.9	8.9
				Mean	61.5	154.3	37.4	10.8	7.7	6.8
Massey Creek	145° 34'	17° 37'	22	Min	37	42	21	6.4	4.8	5.4
				Max	97	248	61	17	13.1	10.1
				Mean	72.8	168.0	44.5	12.6	8.0	7.7
Millaa Millaa Lookout	145° 34'	17° 31'	4	Min	59	144	35	11	7	7
				Max	92	195	59	16	15	10
				Mean	73.0	168.7	51.0	13.0	10.2	8.1
Reynolds	145° 34'	17° 33'	6		90	225	60	14	14.8	7.5
Woolward 1	145° 36'	17° 37'	1		84	231	48	15.7	8.7	9
Woolward 2	145° 36'	17° 37'	1		78	220	47	13.8	7.3	8.4
Total mean					70.41	167.9	43.51	12.38	8.29	7.5
Total min					36	42	21	6.4	4.8	4.7
Total max					97	248	61	17	15.9	10.1

FIRST RECORD AND DESCRIPTION OF *CATATROPIS INDICUS* SRIVASTAVA 1935 (DIGENEA: NOTOCOTYLIDAE), IN AUSTRALIA

MAREE KOCH

Koch, M. 2002 5 31: First record and description of *Catatropis indicus* Srivastava 1935 (Digenea: Notocotylidae), in Australia, *Memoirs of the Queensland Museum* 48(1): 147-153, Brisbane. ISSN 0079-8835.

Each life cycle stage, except the miracidium, of *Catatropis indicus* Srivastava 1935 is described in Australia for the first time. The life cycle was completed experimentally by feeding metacercariae from naturally infected snails, *Gabbia australis* (Bithyniidae), to domestic ducks, *Carrina moschata*. Metacercariae obtained by infecting laboratory-bred snails (*Gabbia australis*) with eggs in faeces of wild *Anas superciliosa*, (Pacific Black duck) were also fed to domestic ducks. Adult trematodes were found in the intestinal caecae of the ducks. Chickens and rats could not be infected. Eggs are operculate with two polar filaments. Sporocysts attach to the lower outer wall of the oesophagus and intestine of *G. australis*. Mother rediae are found on the intestine. Daughter rediae and cercariae develop in the gonads of *G. australis*. Metacercariae remain viable for four months. Comparison with all other known species of *Catatropis* shows that this species resembles most closely *Catatropis indicus* from India in all morphological and life cycle aspects. Slight differences in size can be attributed to geographical variation. □ *Notocotylidae*, *life cycles*, *Bithyniidae*, *Catatropis indicus*.

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Research in Australia on the digenean family Notocotylidae is limited to work done by Nicoll (1914), Johnston (1928), Smith & Hickman (1983), and Cribb (1991). The family contains 3 principal genera, mainly found in birds with aquatic affinities. Adult *Catatropis* is characterised by ventral glands consisting of a uniform median ridge and, in most species, lateral papillae (Yamaguti, 1971), whereas closely related *Notocotylus* has 3 rows of ventral individual papillae (Cribb, 1991). *Paramonostomum* has no papillae or glandular ridges ventrally (Yamaguti, 1971). *Catatropis indicus* Srivastava, 1935 has been recorded from Kuala Lumpur, Malaysia (Rohde & Onn, 1968) and India (Tandon & Roy, 1996). In this paper, each stage of the life cycle of this species is described from Australia for the first time and its taxonomic relationships are discussed.

METHODS

Snails, *Gabbia australis* (Bithyniidae), were collected from dams and water courses in the New England region of New South Wales, and dissected to study intramolluscan stages of the trematode life cycle. Three sets of concurrent life cycle experiments were conducted. In the first, 10 chickens (*Gallus gallus domesticus*) aged 2 weeks, and 9 ducklings (*Carrina moschata*) aged 10 days, and 10 rats aged 4 weeks, were each fed

live snails with 20 metacercariae (aged 14 days) attached to the shells. Animals were autopsied at 17, 23, 39 and 40 days post infection.

In the second experiment, the viability of metacercariae over time was tested. Metacercariae gathered from the same sites as experiment one, were housed in the laboratory under simulated natural conditions. At age 4, 8, 16, 20, 24 and 28 weeks, the metacercariae were fed to 6 ducklings (*C. moschata*) aged 10 days. Each duck received 20 metacercariae and were autopsied at 23 days post infection. In the third experiment, fresh faeces obtained from wild ducks, *Anas superciliosa*, at the sites in experiments 1 and 2, were screened for trematode eggs which were then fed to aquaria of laboratory-bred parasite-free adult snails of *Physa*, *Glyptophysa*, *Austropeplea* and *G. australis*. Metacercariae thus produced were fed at age 14 days, to 4 ducks (*C. moschata*) aged 4 weeks. The ducks were autopsied at 23 days post infection.

All trematode specimens were studied *in vivo* and then fixed in 10% hot formalin, stained with Grenacher's carmine alum or acetocarmine, dehydrated in an alcohol series, and mounted in Canada balsam. Drawings were done using a camera lucida and body parts were measured with a calibrated eyepiece graticule.

For SEM observations, live specimens were



FIG. 1. Eggs (live) of *C. indicus*. Scale: 0.01mm.

fixed in 10% hot formalin, buffer washed in 0.1M PO_4 (pH 2.2), post-fixed in 1.0% OSO_4 in a 0.1M PO_4 buffer (pH 2.2), and dehydrated through an ascending alcohol series. The worms were then critical point dried and sputter-coated with gold. Specimens were examined with a scanning electron microscope at an accelerating voltage of 15kV.

Representatives of the specimens studied have been deposited with the Queensland Museum, Brisbane (QMG217660–217663). Measure-



FIG. 2. Sporocysts (live) of *C. indicus* attached to buccal mass of *G. australis*. Scale: 0.1mm.

ments are quoted in millimetres and where ranges are shown, the mean is noted in parentheses.

RESULTS

EXPERIMENT 1. 160 adult worms were recovered from 8 of the 9 ducks from the first experiment, and all were located in the intestinal caecae, initially in the proximal sections and moving toward the distal sections with increasing days post infection. No worms were recovered from the chickens or rats.



FIG. 3. Mother redia (live) of *C. indicus*. Scale: 0.1mm.

DESCRIPTIONS

Eggs. The eggs are oval, operculate, and have 2 polar filaments, one at each pole. They were apparent in the faeces of infected ducks at ~17 days post infection. Eggs collected from the faeces of infected ducks were incubated at room temperature in filtered pond water and daily observations made. No miracidia were observed to hatch from the eggs. Serial sectioning through the uterus of an adult worm was done at positions proximal, medial and distal to the ovary. A small degree of miracidial development and increase in egg filament length was observed between the proximal and distal egg stages. (Fig.1).

Egg length: 0.0147–0.027mm (0.025); width: 0.010–0.030mm (0.028), $n=12$. Filament length 0.029–0.132mm (0.081), $n=12$.

Sporocysts. Sporocysts were attached to the external surfaces of the lower oesophagus and intestine of *G. australis*. They contained multiple



FIG. 4. Daughter redia (fixed) of *C. indicus*. Scale: 0.1mm.



FIG. 5. Cercaria (fixed) of *C. indicus*. Scale: 0.1 mm.

developing mother rediae and germ balls. Sporocysts and mother rediae were found only in spring (September–October), suggesting a seasonal occurrence of these life cycle stages. (Fig. 2). L:0.16–0.18mm (0.17); W:0.09–0.10mm (0.095), n=4.

Mother Rediae. Mother rediae were found attached by fine white threads of tissue to the external surface of the intestine of *G. australis*. Germ balls and developing daughter rediae were contained within the body posterior to the short caecum. A posterior caudal appendage was demonstrated in vivo. (Fig. 3). L:0.59–0.62mm (0.61); W:0.20–0.23mm (0.21), n=4.

Daughter Rediae. Daughter rediae were found within, and attached externally by fine white tissue to, the gonads of *G. australis*. They could be distinguished from mother rediae by their brown pigmentation and distinctive embryonic cercariae. A muscular pharynx was visible anteriorly, leading into a short caecum. A birth pore was demonstrated in vivo. (Fig. 4).

L:0.392–0.539mm (0.443); W:0.098–0.176mm (0.125), n=12.

Cercariae. Free cercariae were found in the same tissues in which the daughter rediae occurred. Cercariae had 2 lateral eyespots and 1 diffuse median eyespot. Two excretory trunks of the stenostomate type with the main ducts united across the anterior part of the body, opened into the posterior excretory bladder.

Encystment. Cercariae were observed exiting the snails via the mantle cavity. With their tails raised over the top of their bodies, vigorous side-to-side movement instigated a forward swimming direction. Various snail shells were examined for 10–20 minutes prior to an encystment site being chosen, with preference shown for the operculum and inner shell lip. Cercariae manually dissected

from snails encysted on walls or bases of cavity blocks after a period of free swimming ranging from ten seconds to one minute. During encystment, the cercariae attached themselves to the substrate via the adhesive organs on two caudal appendages, and using anterior to posterior body undulations, exuded cyst walls from central dorsal cytogenous glands for 30 seconds. The tail then detached as the cercariae performed 3 to 5 rotations (360°) anticlockwise prior to settling in position within the cyst. (Fig. 5). Body length:0.333–0.382mm (0.355). Tail length:0.353–0.392mm (0.372), n=20.

Metacercariae. Metacercariae were hemispherical in side view, with the attached portion being flat and the free surface convex. There appeared to be two layers of cyst wall.

Cyst diameter:0.157–0.162mm (0.159), n=20. (Figs 6, 7).

Adult. Body elongate and flat, and rounded posteriorly, lacking spines or scales. Adults concave ventrally in vivo. Ventral glands arranged in one continuous median ridge and two lateral rows of 10–12 single glands which run from slightly anterior to the seminal vesicle to just posterior to the ovary. Ventral papillae with two or more splits in surface. Intestinal caecae terminate posterior to the ovary, with the excretory bladder between the testes. Ovary medial, anterior to the excretory bladder and twin-lobed. Mehlis' gland immediately anterior to the ovary. Excretory vesicle posterior to ovary. Vitellaria extend in two lateral groups from the middle of the body to anterior end of the testes. Testes symmetrical and placed posteriorly on both sides of the ovary. Uterus strongly coiled between the cirrus pouch and the Mehlis' gland, intercaecal and overlapping the caeca on both



FIG 6. Metacercaria (fixed) of *C. indicus*. Scale: 0.1mm.

sides. External seminal vesicle posterior to cirrus pouch and strongly coiled. Cirrus pouch containing seminal vesicle and ejaculatory duct. Common genital pore ventral and immediately posterior to oral sucker. Tegument surrounding the genital pore and the ventral surface between papillae covered with many uniformly raised tegumental processes with rounded tips. Excretory pore opens dorsally approximately level with the posterior margin of the testes. SEM of the dorsal surface shows no obvious sensory or tegumentary specialisations. Tegument surrounding the oral aperture studded with scattered rounded unciliated papillae, probably sensory. The rim of the oral sucker with radially orientated folds. (Figs 8 - 10). Measurements of

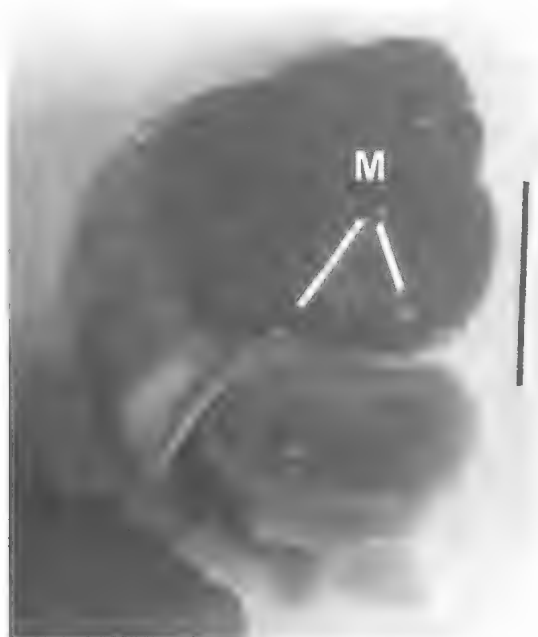


FIG 7. Metacercariae attached to shell of *G. australis* (live). Scale: 1.0mm.

adults removed from the ducks and fixed in 10 % hot formalin are detailed in Table 1.

EXPERIMENT 2. Metacercarial viability was demonstrated to extend from 4 weeks to 16 weeks post-encystment only. 20 adult worms were consistently produced from each age bracket of viable metacercariae.

EXPERIMENT 3. Intramolluscan stages of *C. indicus* were found in 3 locations in the New England Tablelands. The eggs of *C. indicus* were retrieved from faeces of *A. superciliosa* at each of

TABLE 1. Measurements of adult worms (*C. indicus*) fixed in 10% hot formalin (mm), n = 20.

Age of Infection	17 Days	23 Days	39 Days
Length	1.98 - 2.20 (2.09)	2.45 - 2.70 (2.58)	2.70 - 3.40 (2.95)
Max. breadth	0.753 - 0.784 (0.769)	0.88 - 1.07 (0.975)	0.88 - 1.16 (1.01)
Oral Sucker length	0.125 - 0.157 (0.141)	0.11 - 0.167 (0.138)	0.094 - 0.172 (0.133)
max. breadth	0.125 - 0.157 (0.141)	0.157 - 0.167 (0.162)	0.125 - 0.147 (0.136)
Testes length	0.408 - 0.44 (0.424)	0.50 (0.50)	0.50 - 0.69 (0.574)
max. breadth	0.19 - 0.22 (0.205)	0.19 - 0.22 (0.205)	0.25 - 0.28 (0.26)
Ovary length	0.125 - 0.19 (0.041)	0.157 - 0.177 (0.167)	0.174 - 0.28 (0.225)
max. breadth	0.125 - 0.157 (0.016)	0.16 - 0.22 (0.19)	0.19 - 0.22 (0.20)
Cirrus Pouch length	0.063 - 0.063 (0.063)	0.014 - 0.05 (0.045)	0.343 - 0.941 (0.642)
max. breadth	0.44 - 0.502 (0.471)	0.561 - 0.60 (0.582)	0.721 - 0.91 (0.837)
Vitellaria length	0.47 - 0.502 (0.486)	0.60 (0.60)	0.753 - 0.972 (0.857)

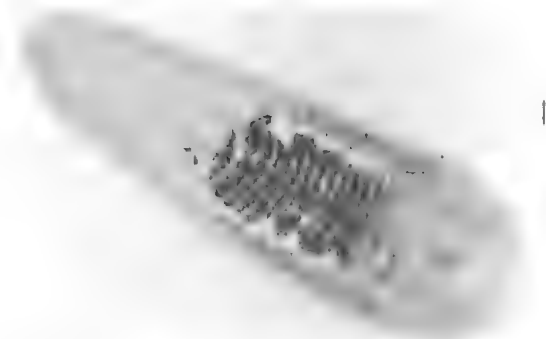


FIG. 8. Adult (fixed) of *C. indicus*. Scale: 0.1mm.

these sites. Adult worms were recovered from the intestinal caecae of all 4 experimental ducks and were identical both in morphology and location within the host, to those adult worms recovered in experiment 1. In the laboratory, intra-molluscan stages of the parasite could only be established in *G. australis* snails.

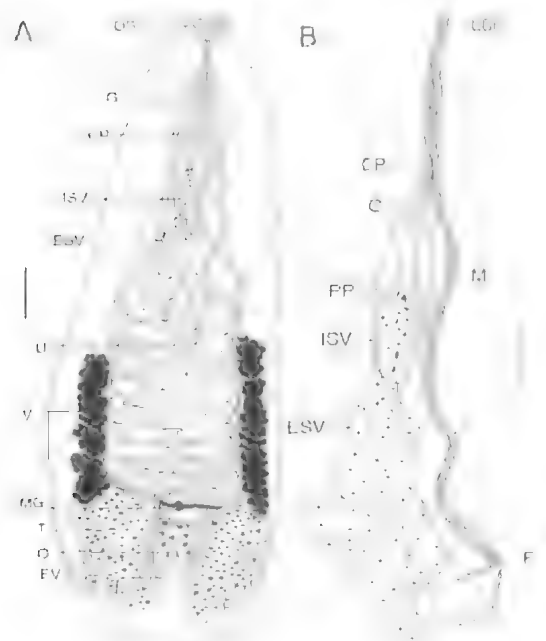


FIG. 9. Schematic drawings of *C. indicus*. A. Adult – internal anatomy. B. Terminal genitalia. C. cirrus: CGP, common genital pore; CP, cirrus pouch; E, eggs; ESV, external seminal vesicle; EV, excretory vesicle; G, gut; ISV, internal seminal vesicle; M, metraterm; MG, Mehlis' gland; O, ovary; OS, oral sucker; T, testes; U, uterus; V, vitelline follicles. Scale lines: 0.1mm.

DISCUSSION

SEM work on this species confirmed a uniform median ridge with lateral papillae, thus placing it in *Catatropis* (Notocotylidae, Digenea). The Australian species differs from others in the same genus in the following aspects. *Catatropis nicolli* (Cribb, 1991) does not have lateral ventral papillae, and its definitive host is a mammal, the water rat *Hydromys chrysogaster*. The description of *C. lagunae* from France by Baysade-Dufour et al., (1996), details 2 significant differences between it and the Australian species. There are fewer lateral papillae in *C. lagunae* (6–9 only), and a voluminous external seminal vesicle was demonstrated using TEM techniques. Although the general anatomy and morphology of my specimens are similar to *C. verrucosa* from Bulgaria (Kanev et al., 1994), it cannot be placed in the same species. This description of *C. verrucosa* is of a much larger species with tegumental spines and its life cycle was completed experimentally in chickens.

Rohde & Onn (1968) described *C. indicus* Srivastava 1935 from Kuala Lumpur as possessing tegumental spines. They could successfully infect both chickens and ducks. All life cycle stages are slightly larger in size than those of my species, and both the number of lateral papillae (12–13) and the location of sporocysts on the buccal mass and oesophagus in their snail host are different to the characteristics described in my experiments.

Srivastava (1935) described only adult specimens removed from the intestinal caecae of the Indian fowl, *Gallus bankiva murghi*. Life cycle comparisons cannot be drawn with his original classification. However, Srivastava stated the ratio of the length to the maximum breadth of the body of his specimens as 4:1. Adult worms from my experiments and those described by Tandon & Roy (1996), also from India, exhibit a body length to maximum breadth ratio of 2:1, suggesting that Srivastava's specimens may have been more mature.

Catatropis indicus from India (Tandon & Roy, 1996) differs from the Australian species only slightly in length (~0.01–0.2mm) in some life cycle stages. Geographical variability can be responsible for this, and, as there are no significant morphological and life cycle differences, I cannot justify the a new species for the Australian specimens. Thus, I tentatively place my specimens in *C. indicus* (Tandon & Roy, 1996). Slight morphological variations amongst

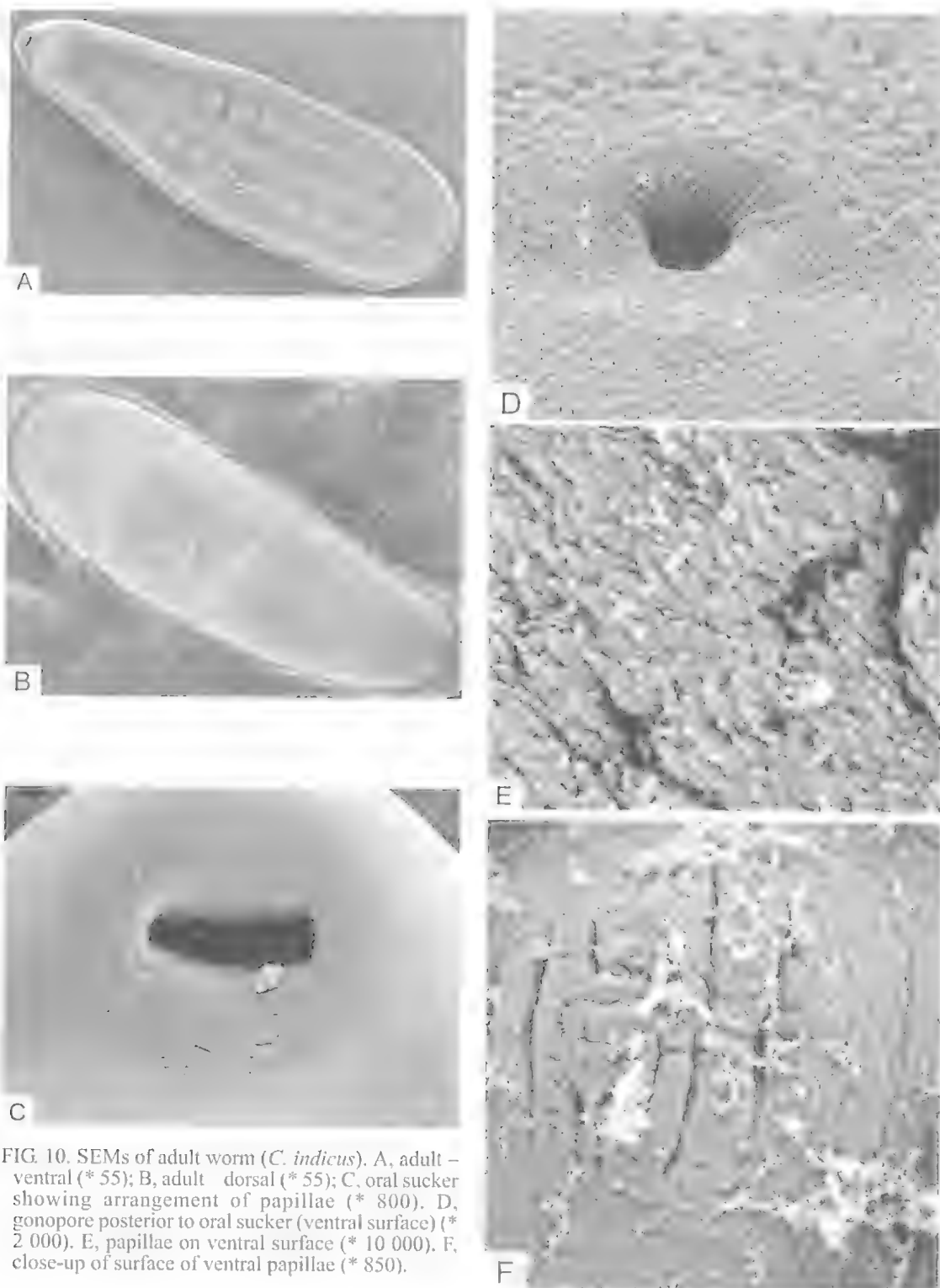


FIG. 10. SEMs of adult worm (*C. indicus*). A, adult – ventral (* 55); B, adult – dorsal (* 55); C, oral sucker showing arrangement of papillae (* 800). D, gonopore posterior to oral sucker (ventral surface) (* 2 000). E, papillae on ventral surface (* 10 000). F, close-up of surface of ventral papillae (* 850).

members of a species can be expected. rDNA sequencing of adult worms from my experiments currently in progress in conjunction with Littlewood & Olsen (2001), will hopefully enable taxonomic placement of this species and provide insight into the evolutionary steps taken by the trematode in its journey to cross continents.

As *G. australis* is a member of the Bithyniidae, (Beesley et al., 1998) and the snail host of *C. indicus* in Malaysia and India (*Bithynia siamensis*) also belongs to this family (Fretter & Graham, 1962), the trematode appears to be specific to different species of different genera belonging to the same family. The range of *G. australis* extends throughout central and western NSW and into the NT (Ponder, et al., 2000), concurrent with the range of *A. superciliosa* (Simpson & Day, 1993). Future sampling will confirm the range of *C. indicus* in this country and the depth of its final host specificity. Other ducks similar in physiology and habitat useage may also be vulnerable (e.g. *Biziura lobata*, *A. gibberifrons*, *Aythya australis*).

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LITERATURE CITED

- BAYSSADE-DUFOUR, C., ALBARET, J., FERMETQUINET, H. & FARHATI, K. 1996. *Catatropis lagunae*, n. sp., Trematoda, Notocotylidae, parasite of seabirds [French]. Canadian Field-Naturalist 110: 392-402.
- BEESELEY, P., ROSS, G. & WELLS, A. (eds) 1998. Mollusca: the southern synthesis. Fauna of Australia. Vol 5. (CSIRO Publishing: Melbourne).
- CRIBB, T. 1991. Notocotylidae (Digenea) from the Australian water rat *Hydromys chrysogaster* Geoffroy, 1804 (Muridae). Systematic Parasitology 18: 227-237.
- FRETTER, V. & GRAHAM, A. 1962. British Prosobranch molluscs – their functional anatomy and ecology. (Ray Society Publications: London).
- JOHNSTON, T.H. 1928. New trematodes from the Australian waterhen, *Gallinula tenebrosa*. Records of the South Australian Museum 1: 135-142.
- KANEV, I., VASSILEV, I., DIMITROV, V. & RADEV, V. 1994. Life-cycle, delimitation, and redescription of *Catatropis verrucosa* (Frolich, 1789) Odhner, 1905 (Trematoda: Notocotylidae). Systematic Parasitology 29: 133-148.
- LITTLEWOOD, D.T.J. & OLSON, P. 2001. Small subunit rDNA and the Platyhelminthes: Signal, noise, conflict and compromise. Pp. 262-278. In Littlewood, D.T.J. & Bray, R. Interrelationships of the Platyhelminthes. (Natural History Museum: London).
- NICOLL, W. 1914. The trematode parasites of north Queensland. II. Parasites of birds. Parasitology 7: 105-126.
- PONDER, W.F., CLARK, S.A. & DALLWITZ, M.J. 2000. Freshwater and Estuarine Molluscs. An interactive illustrated key for New South Wales. (CSIRO Publishing: Sydney).
- ROHDE, K. & ONN, L.F. 1968. Life cycle of *Catatropis indica* Srivastava 1935. Zeitschrift für Parasitenkunde 30: 137-148.
- SIMPSON, K. & DAY, N. 1993. Field guide to the birds of Australia. (Penguin Books: Sydney).
- SMITH, S.J. & HICKMAN, J.L. 1983. Two new Notocotylid trematodes from birds in Tasmania and their life histories. Papers and Proceedings of the Royal Society of Tasmania 117: 85-103.
- SRIVASTAVA, H.D. 1934. On a new species of *Catatropis* Odhner, 1905, from an Indian fowl – *Gallus Bankiva murghi*. Proceedings of the Indian Academy of Science 4(3): 283-287.
- TANDON, V. & ROY, B. 1996. Stereoscan observations on the tegumental surface of *Catatropis indicus* Srivastava 1935. Acta Parasitologica 41: 115-119.
- YAMAGUTI, S. 1971. Synopsis of digenetic trematodes of vertebrates. Vols 1 & 2. (Keigaku Pub. Co.: Tokyo).

SOUTHERLY RANGE EXTENSION FOR COMMON ROCK-RAT *ZYDOMYS ARGURUS* (RODENTIA: MURIDAE) IN QUEENSLAND. *Memoirs of the Queensland Museum* 48(1): 154. 2002:- The Common Rock-rat (*Zydomys argurus* Thomas, 1889) is a small to medium-sized rodent upto 55g; it is almost always associated with rocky outcrops (Fleming, 1995); it is endemic to N Australia (WA, NT, QLD); in QLD it occurs in rocky ranges and outcrops between Lagoon Creek Gorge, (17°33'S, 138°01'E) and Cape Melville, (14°22'S, 144°37'E) to Lark Quarry, (23°01'S, 142°24'E) and Blackdown Tableland, (23°44'40"S, 149°06'20"E) (Kitchener, 1989; QM data).

In May 2000 a trapping survey for Northern Quoll (Oakwood & Firestone, 2000), in the Mount Moffatt Section of Carnarvon NP, 600km NW of Brisbane used wire cage, and Type A and Type B Elliott traps set at 7 sites (454 trap nights) on or near rocky outcrops. Traps were baited with a bolus of rolled oats and peanut butter, or salami laced with pistachio essence. *D. hallucatus*, Fawn-footed Melomys *Melomys cervinipes*, Long-nosed Bandicoot *Perameles nasuta*, *Pseudomys* sp. and *Z. argurus* were caught.

This new record for *Z. argurus* was caught at The Duchess (25°06'11.6"S, 147°51'06.6"E), a distinctive outcrop of Precipice Sandstone overlooking the Maranoa River and rising above the surrounding sandplain to an altitude of 740m. Two *D. hallucatus* and one unidentified rodent were also caught at this site (116 trap nights). *Z. argurus* was captured on 30 May 2000 in a collapsible wire cage trap (55.5x20x20cm), baited with peanut butter and rolled oats. The trap was set at the entrance of a cave in the vertical rock-face, on a broad ledge just below the summit. The cave faces SW, is up to 2.0m high, 1.55m wide and 13.8m long. No evidence of *Z. argurus*, such as scats or chewed seeds and fruit, was observed in the vicinity of the trap site.

Vegetation in the trap site is scattered *Angophora leiocarpa* and *Eucalyptus decorticans*, with a mid-layer dominated by *Leptospermum lamellatum*, *Acacia* spp., *Callitris endlicheri* and low shrubs. The ground layer is dominated by *Lomandra* sp., while other graminoids and forbs are sparse. Dense leaf litter covers the ground. Areas of vertical rock-face are dominated by *L. lamellatum*, *Wahlenbergia islensis*, and bryophytes. The area equates to regional ecosystem 11.10.4 'complex of *Eucalyptus decorticans* and/or *Acacia shirleyi* woodland/open forest and mixed woodland/open forest on Cainozoic to Proterozoic consolidated, medium to coarse grained sediments' (Young et al., 1999). This habitat type is extensive in Mount Moffatt, Moolayember, Salvator Rosa and Goodliffe Sections of Carnarvon National Park, and is broadly consistent with habitat records for *Z. argurus* in other parts of Queensland.

Z. argurus was extremely active in the trap when first approached and the tip of the tail was discarded when the animal was first handled. The voucher specimen, lodged in the Queensland Museum (QMJM 14298), is a juvenile male, with SVL ~85mm and tail length ~87mm. Its body has brownish-grey fur above, buff on the sides and cream below. The tail is distinctly bicoloured (dark grey above, light grey below) and slightly, but noticeably swollen near the base, clearly ringed (as opposed to mosaic) and well furred. The nose is pink, ears dark grey and feet dark grey, furred white above. The specimen was distinguished from the other 8 eight species of rodent that occur at Mount Moffatt by a

combination of body size, SVL/tail length ratio, un-notched upper incisors, strongly bi-coloured well furred tail which is swollen at the base, and pronounced roman-nose.

The southern limit for *Z. argurus* was Blackdown Tableland (23°44'40"S, 149°06'20"E) where it was trapped between Peregrine and Horseshoe Lookouts, Sept.1984 (C. James, G. Porter pers. comm.). This record in the Carnarvon Range represents a range extension of 200km. The climate of Carnarvon Range is subhumid, with mean annual rainfall of >800mm (Galloway et al., 1974). The vertebrate fauna is predominantly Bassian whereas *Z. argurus* is one of a small subset (7 spp.) of Torresian species.

Zydomys argurus is regarded as secure at a national level (Lee, 1995), and common in Queensland (Dickman et al., 2000).

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Literature Cited

- DICKMAN, C.R., LEUNG, L. K.-P & VAN DYCK, S.M. 2000. Status, ecological attributes and conservation of native rodents in Queensland. *Wildlife Research* 27: 333-346.
- FLEMING, M. 1995. Common Rock-rat *Zydomys argurus*. Pp. 620-621. In Strahan, R. (ed) *The Mammals of Australia*. (Australian Museum/Reed: Sydney).
- GALLOWAY, R.W., GUNN, R.H., PEDLEY, L., COCKS, K.D. & KALMA, J.D. 1974. Lands of the Balonne-Maranoa area, Queensland. Land Research Series No. 34. (CSIRO: Melbourne).
- KITCHENER, D.J. 1989. Taxonomic appraisal of *Zydomys* (Rodentia, Muridae) with descriptions of two new species from the Northern Territory, Australia. *Records of the Western Australian Museum* 14: 331-373.
- LEE, A.K. 1995. The Action Plan for Australian Rodents. (Australian Nature Conservation Agency: Canberra).
- OAKWOOD, M. & FIRESTONE, K. 2000. Conservation and Management of the Northern Quoll *Dasyurus hallucatus*. Unpublished report to the Queensland Parks and Wildlife Service.
- YOUNG, P.A.R., WILSON, B.A., McCOSKER, J.C., FENSHAM, R.J., MORGAN, G. & TAYLOR, P.M. 1999. Brigalow Belt. Chapter 11. In Sattler, P.S. & Williams, R.D. (eds) *The Conservation Status of Queensland's Bioregional Ecosystems*. (Environmental Protection Agency: Brisbane).

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FRESHWATER TURTLE POPULATIONS IN THE AREA TO BE FLOODED BY THE WALLA WEIR, BURNETT RIVER, QUEENSLAND: BASELINE STUDY

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A baseline turtle study was requested in a review of impacts of changed water levels to follow construction of the Walla Weir on the Burnett River (25°02'S, 152°04'E) at Wallaville, Queensland. Four species of freshwater turtle occur in the area. *Emydura krefftii* was abundant throughout most of the Walla Weir area. This population's characteristics indicate poor recruitment or survivorship of young turtles, even though adults breed at a very high rate; a size class distribution skewed towards adults; a sex ratio of 1:1; and almost all adults breeding annually. The straight carapace length (SCL) at which 50% of the population had matured to adult status was used to define size at first breeding and was 18.9cm for males and 21.1cm for females. Mean of all adults was SCL = 22.9cm for males and 25.1cm for females. Length/weight analyses measure health and body condition for each sex. *Elseya* sp. was uncommon in the area and was mostly concentrated in a single pool. *Elseya* sp. has a well-developed cloacal gill system. Its population structure indicated that the population was not performing well. Captured turtles comprised large adults and a group of immature turtles born in about 1990-1991. Recruitment of young appears to be limited. *Chelodina expansa* and *Elseya latisternum* occurred at very low density in the study area. A set of parameters to describe population performance of chelid turtles and suitable for short-term studies is identified; size class distribution by sex and maturity; and size at first breeding, mean size of adults, annual breeding rate, and length/weight condition curves for each sex. □
Freshwater turtle, population, Walla Weir, Burnett River, Queensland.

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As a result of opinions expressed during the environmental impact assessment of the proposed Walla Weir on the Burnett River (25°02'S, 152°04'E), the Commonwealth Minister for the Environment commissioned a review of information relating to the impact of such weir on the lungfish, *Neoceratodus forsteri*, and the undescribed freshwater turtle, *Elseya* sp. This review (Boardman, 1996) concluded that the weir was unlikely to impact significantly on the lungfish and that only a small part of the total distribution of the turtle would be affected. However, this same review identified the cumulative impacts of present and future dams and weirs in the Burnett R. as a more significant issue, and recommended that a long-term program be established to collect baseline data on the lungfish and *Elseya* in the Burnett, Mary and Fitzroy River systems. The present study was undertaken in response to this and was part of a larger study to investigate the impact of dams and weirs on freshwater turtles in the Fitzroy, Burnett and Mary River catchments.

The Australian freshwater turtle fauna is dominated by Chelidae and species taxonomy is still

being resolved (Georges, 1994; Manning & Kofron, 1996; Cann, 1998). Chelid turtles are long-lived (Kennett, 1994; Parmenter, 1985) and there are few long-term studies of Australian freshwater turtles, except for *Pseudemydura umbrina* (Kuchling & Bradshaw 1993; Kuchling et al., 1992), that can address the dynamics of populations in response to threatening processes. Gathering comprehensive demographic data for turtles can be expected to take decades (Gibbons, 1989; Congdon et al., 1993), although the process could be quicker with rapidly maturing species such as *Chelodina rugosa* (Kennett, 1994). By contrast, and in the context of planning for the increasing demand for water for agricultural and pastoral use in south and central Queensland, answers to questions concerning the impact of dams and weirs on turtle populations are required in the immediate future. Resolving these conflicting time scales lies at the crux of the problem when attempting to provide freshwater turtle baseline data as recommended by Boardman (1996).

With the limited time available before the anticipated elevation of water levels in the Walla

Weir in late 1997, it was impracticable to plan for long term ecological studies for the site. In addition, extended rains with elevated water flow in the Burnett R. hindered turtle capture during November 1996 - April 1997 and curtailed study during the one breeding season available within this baseline study period.

A description of population dynamics with respect to age structure, size distribution, sex ratio, maturity ratio, annual breeding rates, fecundity and survivorship provides more information on how a population is performing than studies that focus on census and distribution. A rapid assessment method targetting key parameters was needed for the baseline study of *Elseya* sp. before water levels rose. Not all population dynamics parameters would be equally useful. For example, no validated method for age determination of Australian freshwater turtles existed, while survivorship measurements would require some years of mark-recapture studies. In-depth studies of a population through several breeding seasons would be needed to quantify inter-annual variability of fecundity with respect to eggs per clutch, clutches per season and incubation success of clutches. However, short term sampling of turtles in an area should be able to describe a population with respect to size, sex, maturity and breeding status of the individuals. From these data it is possible to quantify a range of population parameters including sex ratio, size class distribution by sex, size at which each sex reaches adulthood, mean size of breeding adults and annual breeding rate of adults of each sex. These are demographic parameters that can be measured within a single year and have the potential to change in response to long term changes in living conditions and health of the turtles. When compared across time, they should detect changes in population function. For example, Kuchling & Bradshaw (1993) recorded that ovulation and egg production of captive *P. umbrina* was easily suppressed under stress or sub-optimal conditions. While not immediately informative, other than to ensure that the same animal was not counted twice, establishment of tagged populations facilitates investigation of other demographic parameters such as growth, dispersal, migration and survivorship across the years after the rise in water level.

However, results from short term studies must be used cautiously. There are few databases for chelid turtles against which to judge how such parameters may vary in response to changing climate, independent of any changes due to dam

or weir construction (Kennett & Georges, 1990). Turtle population structure is not completely dependent on in-river processes (Thomson, 1983). Anthropogenic terrestrial influences (independent of the aquatic environment) may have significant impact on turtle population dynamics during the terrestrial phase of egg incubation. For example, predation of eggs and hatchlings by foxes or pigs, trampling of nesting banks by stock or overgrowth of nesting banks by weeds could reduce hatchling recruitment. Therefore, it is highly unlikely that there is a short term solution to understanding the impact of dams and weirs on conservation of freshwater turtles.

This baseline study was to examine freshwater turtles in the proposed Walla Weir area of the Burnett R. prior to the rise in water level. The turtles were investigated from the perspective of population function using analyses addressing sex, maturity and breeding status of measured individuals from within a tagged population. While maintaining a general approach to address all species present, special emphasis was placed on *Elseya* sp.

METHODS

Specific nomenclature follows Georges & Adams (1992), Georges (1994) and Cann (1998). *Elseya* sp. in the Burnett R. is treated as an undescribed species resembling *Elseya dentata* from the Northern Territory (*Elseya* sp. aff. *dentata* [Burnett]). Georges & Adams, 1996). This species in the Burnett and adjacent rivers is being described as new (S. Thomson, personal communication.). A voucher specimen of the species has been registered in the Queensland Museum: J67876. Although *Emydura krefftii* may be synonymous with the widely dispersed polytypic *E. macquarii* (Georges & Adams, 1992, 1996; Georges, 1994), formal taxonomic revision accounting for these genetic studies has yet to be completed. Until it is we use *Emydura krefftii* for the Burnett R. population.

Where water clarity permitted, turtles were hand captured while snorkelling by day or using spotlighting at night. In turbid water, turtles were captured using seine nets, dip nets or funnel traps. The seine nets (30m length, 3m fall, 15cm mesh size) were dragged through large pools and, because of the mesh size, captured only large immature turtles and adults. These nets were inefficient in those sections of the river with depths exceeding the fall of the net. Dip nets were scooped through shallow areas of dense aquatic vegetation in search of small turtles. A range of

size and design of funnel traps were used and were baited with bread or punctured cans of sardines in vegetable oil. Traps were set completely submerged and checked at 1-2hr intervals or were set partly submerged to permit trapped turtles or platypus to breathe and checked at 2-4hr intervals. Following their capture, turtles were held in bags or plastic bins in the shade for up to 24hr and processed for tagging, measurements, and gonad examination. Turtles were released at their respective capture sites.

Linear measurement of turtles were made with vernier slide callipers ($\pm 0.01\text{cm}$) or, for large turtles, with wooden callipers and a steel rule ($\pm 0.1\text{cm}$). Straight carapace length (SCL) was measured from the anterior midline margin of the carapace to the posterior midline margin of the carapace. Straight carapace width (SCW) was measured at the widest part of the carapace perpendicular to the midline axis of the carapace. Plastron length (PL) was measured from the middle anterior to the middle posterior of the plastron. Plastron width (PW) was measured perpendicular to the midline axis of the plastron immediately anterior to the bridges. Head length (HL) was measured from the anterior tip of the maxillary sheath of the jaw to the posterior tip of the supra-occipital process. Head width (HW) was measured across the widest part of the head behind the ears at the quadrate bones. Tail measurements were taken from the tip of the firmly out-stretched tail to the plastron (TLP), to the anterior of the vent (TLV) and to the posterior mid-point of the carapace (TLC). Turtles were weighed with either a 10kg or 15kg hanging spring balance ($\pm 0.1\text{kg}$) or with a 2kg top-pan electric balance ($\pm 1\text{gm}$). Plastron curvature was scored as concave, convex or flat by inspection with a straight edge laid over each of the length and width of the mid plastron.

Each turtle was individually identified with one or both of the standard freshwater turtle tagging systems used in the Queensland Turtle Research Project. Numbered self piercing, self locking, monel tags originally designed as chicken wing bands (National Band and Tag Company, Newport, Kentucky, USA) were applied through the webbing between digits 4 & 5 of a rear foot of the turtle. For small turtles with $\text{SCL} < 15\text{cm}$, the tag was not applied through the webbing of the hind foot but was applied through marginal scute 11 counting from the anterior. Most turtles received a coded carapace notching: marginal scutes of the carapace are assigned a

letter code in order from the right front in a clockwise direction; one or more notches are cut into the marginal scutes each to a depth of approximately one third of the width of the scute to provide a series of coded turtles a,b,c,z,ab,ac,ad,.....,az,bc,bd, abc,.... ; the nuchal was not used for notching; no more than one notch was applied per marginal scute.

Gonads and associated reproductive ducts of live turtles were examined visually to determine sex, maturity and current breeding status using laparoscopy with a Carl Storz 26031B or 28300B Hopkins telescope, depending on the size of the turtle, connected to a Carl Storz 482B cold light source and inserted through a 7mm or 3mm o.d. cannula, respectively. Access to the abdominal cavity was achieved via a small scalpel cut in the skin adjacent to the anterior ventral margin of the right inguinal area. The cut was limited to ensure a firm fit of the cannula. Throughout the examination the turtle was firmly hand held vertically with its head downwards. The turtle's right leg was manually distended posteriorly to minimise disturbance of the instruments. On completion of the examination, the cut to the skin was closed with an absorbable suture (catgut chromic #3). Instruments were stored in and used from a 70% ethanol bath. The inguinal area was scrubbed with 70% ethanol prior to making the incision. To facilitate viewing of the organs, the abdominal cavity was inflated with air, as required, from a hand-operated pump. This methodology follows closely that developed for similar studies with crocodiles and marine turtles (Limpus, 1984, 1992; Limpus & Reed, 1985; Limpus et al., 1994a,b). Sex was determined by the presence of either an ovary or testis. Immature females were recognised by their straight or partly enlarged (partly convoluted) oviducts that were circular to oval in cross-section and an unexpanded ovary. Adult females were characterised by the presence of one or more of the following: enlarging vitellogenic follicles; mature follicles; corpora lutea, corpora albicantia or large atretic follicles in an expanded ovary. Oviducal egg may be present in the adult female. A flattened and greatly convoluted oviduct was a feature of all adult females identified by the above criteria and was used in assigning adult status to turtles that have completed enlargement of the ovary but displayed no signs of present or past breeding activity. Immature males had the epididymus still within the body wall or incompletely enlarged from the body wall while adults had an

epididymus that was enlarged and pendulous from the body wall. The presence of oviducal eggs identified by palpation was used to identify adult females among turtles whose gonads were not viewed. Large short-tailed turtles selected for palpation were held vertically with the head upwards while shaking them gently and at the same time squeezing fingers firmly into the inguinal areas to feel for oviducal eggs.

Using dose-effect terminology, the size at which 50% of the turtles are sexually mature can be termed 'adult size₅₀' (AS₅₀). The proportion of adult turtles in 1cm size increments for each sex was analysed using simple logistic and gompertz functions to estimate the AS₅₀ values. Goodness of fit was based on residual variance and log likelihood functions.

Eggs laid onto the container floor while a turtle was being held for measurements were placed with minimum rotation in a covered plastic container of sand from a freshwater stream moistened to 6% by weight with freshwater. The container was covered with a thin polythene sheet to minimise water loss and placed in a well ventilated room out of direct sunlight to incubate at "room" temperature. Incubation temperatures were not measured. Eggs and hatchlings were measured with vernier calipers ($\pm 0.01\text{cm}$) and weighed on an electric top-pan balance ($\pm 0.1\text{g}$).

Nomenclature of scutes follows Pritchard & Trebban (1984) except that 'supracaudal' scutes are included in the marginal scute count. Age estimate for small turtles that retained a complete set of growth layers on their scutes, presumed that growth layers are deposited annually.

STUDY AREA

The study area is the main stream of the Burnett R. that will be flooded following construction of the Walla Weir 74.5km upstream from the mouth and approximately 19km downstream from the existing (1997) Bruce Highway traffic bridge at Wallaville. We examined 19 sites (Table 1) over 25km of river extending from 6km upstream of the Bruce Highway bridge downstream to the Walla Weir. These sites are referred to as the Walla Weir area of the Burnett R. The study sites were of irregular length and identified by prominent land marks or natural changes in the stream such as narrow shallow areas between larger pools. Latitudes and longitudes were recorded using a Geographical Positioning System (GPS) recorder.

The dry season stream was continuous, usually 10-20m wide and flowed slowly in a much wider dry sandy to gravel river bed. The dry season stream, usually <3m deep, varied from a few cm to ~6m deep. During floods the stream may be tens of metres deep. The river substrate was compacted sand with few rock outcrops. Only in some of the larger, wider and deeper pools was there a substantial silt substrate. As the stream meandered within the dry season river bed, one bank was usually flanked with a narrow fringe of riparian vegetation, predominantly *Melaleuca*, *Callistemon* and *Casuarina* mixed with a wide range of rainforest species, overhanging the water. Breaks in this narrow fringe of trees were frequently dense with weeds. The opposite bank was usually a shallow sand flat with little vegetation other than young regrowth *Melaleuca* and *Callistemon*, sedges and grasses. This latter bank was heavily trampled and grazed by cattle. Where there were large overhanging trees at the stream margin, there were usually deeply recessed cavities under the bank that were supported by the root mass of the trees. Also where there were large trees on the river bank there were often numerous submerged snags, mainly tree trunks, branches and roots. Fence posts, barbed wire and other agricultural debris frequently were entangled in these snags.

There was considerable variability in the macrophyte community in the river. During December 1994 - January 1995 much of the stream bed was densely overgrown with aquatic macrophytes and in some sites the submerged macrophytes exceeded 2m in height. The high rainfall during the 1995 wet season and subsequent increased river flow removed almost all of these dense macrophyte stands. Substantial regrowth was not in evidence until mid 1997.

Study sites 8-12 were sampled prior to the Boardman (1996) review and a team of snorkellers swam the length of this section once and sites 10-12 an additional five times during December 1994-January 1996. For 10 of the sites (number 8-17) that were continuous over approximately 6km of river, a team of snorkellers swam the length of the section on three separate occasions during July-August 1997. Turtle captures were supplemented by trapping in sites 13-19 during this same period. During the turbid water period in October 1996 - February 1997, sites 1-12 were sampled only by seine-netting, dip-netting and trapping. One site (number 11) was sampled on all sampling trips and using all sampling techniques at various times.

TABLE 1. Study sites sampled during the baseline study of freshwater turtles within the Walla Weir area of the Burnett River. Sites are numbered sequentially from upstream to downstream.

Site number	Latitude & longitude	Maximum depth (m)	Description
1	25°07.99'S, 151°58.99'E	1.5	Impoundment area of a small flow rate weir ~1.5km upstream of proposed bridge site (site 3).
2	25°07.93'S, 151°58.95'E	2	Backwater to main stream, downstream of site 1.
3	-	1	Shallow rocky area 600m upstream from site 4. Rainforest riparian margin on northern bank.
4	-	2	New Bruce highway traffic bridge which replaced the highway bridge which was in use at the time of the study. Firm compacted sand with few rocks or snags.
5	25°07.19'S, 151°59.20'E	2	Main stream 100m downstream of site 4.
6	-	2	Pool at end of small rapids 300m downstream from site 5.
7	-	2	End of the backwater (200m downstream from site 6).
8	-	2	Extends upstream from old traffic bridge for ~750m. Firm sand bottom with few rocks. Narrow stream along northern bank with overhanging trees.
-	25°05.7'S, 151°59.71'E	-	Old Bruce Highway traffic bridge at time of study.
9	-	2	Extends downstream from old traffic bridge for ~300m. Narrow stream on northern bank with overhanging trees.
10	25°04.76'S, 151°59.86'E	2	Narrow stream along northern bank with overhanging trees. Larger pools associated with large fallen trees.
11	25°04.69'S, 151°59.90'E	6	Deep pool on bend of river with structural remains of the water intake system for the old Wallaville Sugar Mill. Within this pool, rock crevices replace the refugia provided by overhanging root masses, fallen logs and snags that occurred in pools upstream. Includes backwater of creek entering from the northern bank.
12	25°04.69'S, 152°00.00'E	1	Continuing downstream from site 11 to the next shallow rapids. (100m downstream of site 11)
13	25°04.31'S, 152°00.15'E	5	Steep sided pool beginning in gravel rapids and terminating in rock outcrop with riffle area. Course gravel and submerged rocks and logs mid stream
14	25°04.42'S, 152°00.29'E	2.5	Starts and finishes at prominent rock outcrops into the stream. Rocky bottom in parts and submerged boulders and logs midstream.
15	25°04.44'S, 152°00.39'E	1.5	Narrow stream along northern bank with overhanging trees; mostly shallow sand bottom with interspersed small pools. Terminates where stream opens out into broad pool of site 16.
16	25°04.56'S, 152°00.56'E	1.5	Broad and mostly shallow, extensive Vallisneria beds; few logs.
-	-	-	Murray's Crossing.
17	25°05.04'S, 152°01.16'E	2	Sandy to course gravel bottom.
18			This section not examined in detail.
19	25°05.26'S, 152°02.15'E	2	Long pool on southern side of "island" adjacent to the end of Pine Grove Park Road. Mud bottom with occasional sand and gravel areas. Terminates on junction with creek entering from the southern bank. Turbid, algal bloom and ~no macrophyte bottom cover in July-August 1997.
-	-	-	Stream area down stream to the Walla Weir construction site. This section not examined in detail. Turbid on all visits.
-	-	-	Walla Weir construction site.

RESULTS

Four species of freshwater turtles were captured in the Walla Weir area. 328 captures was recorded from all methods (Table 2) during December 1994 to August 1997. The capture rate while snorkelling was ~93% of all turtles encountered. *E. krefftii* was the most frequently encountered, accounting for 93.0% of captures. The other 3 species were rarely encountered: *Elseya* sp. 4.3% of captures; *Elseya latisternum* 0.9%; *Chelodina expansa* 1.8%. Only 2 turtles from these latter 3 species were sighted but not captured - a large and a medium sized *Elseya* sp.

All turtles, representing all 4 species, whose gonads were visually examined were distinctly male or female.

Turtles were captured at all 19 study sites. However, at the junction of the 2 sites near the Bruce Highway traffic bridge, tree clearing and bank remodelling had resulted in ~100m of stream with effectively no refugia for turtles. No turtles were seen in the area on any visit. Numerous turtles were seen basking on branches and snags throughout the study area, especially during the cooler months. However, only *E. krefftii* was identified among the basking turtles.

TABLE 2. Frequency distribution by capture method for 328 freshwater turtles in the Walla Weir area. This summary treats multiple captures of the same turtle as separate events.

	<i>Elseya</i> sp.	<i>Elseya</i> <i>latisternum</i>	<i>Emydura</i> <i>krefftii</i>	<i>Chelodina</i> <i>expansa</i>
Snorkelling	14	2	206	2
Seine netting			64	
Dip netting			3	
Trapping		1	26	3
Night spotlighting			1	
Dead carcasses			3	1
Incubated eggs			2	
Total	14 (4.3%)	(0.9%)	305 (93.0%)	6 (1.8%)

EMYDURA KREFFTII

E. krefftii was the most common turtle in the river and was captured or commonly observed basking, foraging or surfacing for breaths at all sites except at the highway bridge. The turtles used fallen trees, holes under the bank supported by roots, overhanging root tangles and large stands of submerged macrophytes as refuges. Medium sized immature and adult turtles were common while few small turtles were recorded. Although the netting method was biased towards large specimens, very small turtles were not observed commonly even while snorkelling. (Turtles as small as 1yr olds are regularly captured while snorkelling in other rivers. CJL unpubl. data). Qualitative observations suggest that smaller turtles were more likely to be found in vegetated shallow, slow moving sections of the stream such as site 16. *E. krefftii* was the only species seen at night in the shallow weed-bed areas in January 1995. By day, these turtles were commonly observed swimming among logs and snags as well as walking on the bottom. Many *E. krefftii* were observed foraging in mid water among tall macrophytes during December 1994-January 1995 and in July-August 1997.

The size class distribution by sex of captured *E. krefftii* (Fig. 1) shows a low frequency of individuals among the smaller size classes. This was recognised during the study, but active searching of a range of microhabitats at different times of the year and the use of a range of capture techniques failed to locate abundant smaller size classes. Only 3 individuals (1.0%) were found with SCL~2.8-11cm. Adult males and females were the most common age class, up to maximum SCL=29.1cm and weight=3.4kg. Sex ratio was not significantly different from 1:1 among the turtles whose sex was determined.

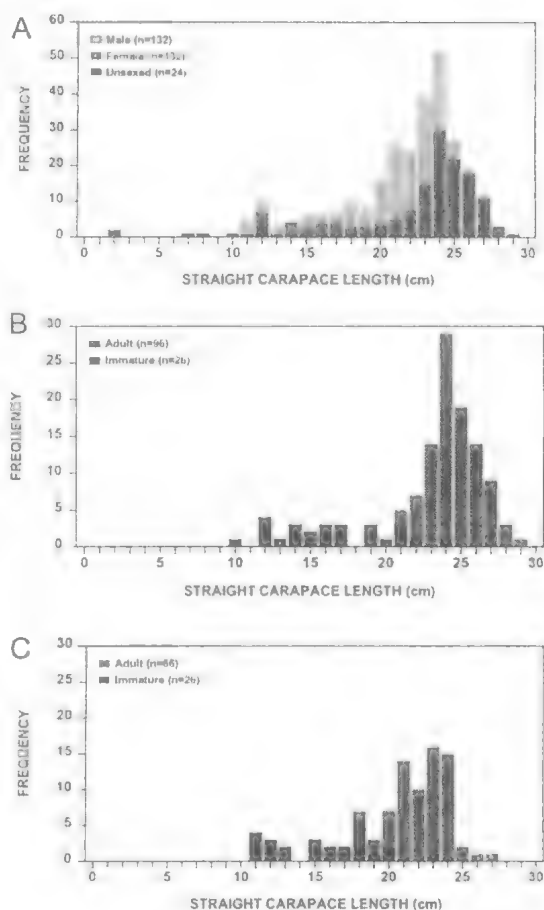


FIG. 1. Frequency distribution by size for *Emydura krefftii* from the Walla Weir area of the Burnett River.

Analysis of covariance showed significant differences between sexes for linear correlation of SCL against width (SCW); plastron length (PL) against width (PW) (Table 3; Fig. 2A,B). Head length and width were not linearly correlated (Fig. 2C). The relationship between SCL and weight was non linear (Fig. 2D). However, there was a significant linear correlation between \log_{10} weight and \log_{10} SCL for each sex and there was a significant difference between the sexes (analysis of covariance: $F_{2,268}=15.49$, $p<0.0005$):

for males, $\log_{10}(\text{weight}) = 2.9243 \cdot \log_{10}(\text{SCL}) - 3.8530$ ($F_{1,140}=6574$; $r^2=0.9792$, $df=140$);

for females, $\log_{10}(\text{weight}) = 3.0553 \cdot \log_{10}(\text{SCL}) - 4.0039$ ($F_{1,128}=4488$; $r^2=0.9723$, $df=128$).

These length/weight relationships provide a measure of general health of *E. krefftii*.

TABLE 3. Linear regression analysis by sex of carapace and plastron measurements of *Emydura krefftii* of all size classes from the Walla Weir area. Analysis of covariance was used to test for differences between sexes for these analyses. Regression analyses results are expressed in the form $y=ax+b$. * testing for coincidental regressions.

Variables		Linear regression analysis							Analysis of covariance*		
x	y	sex	a	b	F	df	p	r ²	F	df	p
SCL	SCW	male	0.576196	3.793748	1589	1,140	<0.005	0.9190	15.90	2,270	<0.0005
		female	0.618611	3.270545	1519	1,130	<0.005	0.9212			
PL	PW	male	0.417151	0.43618	838	1,138	<0.005	0.8587	10.01	2,268	<0.0005
		female	0.438256	0.341042	805	1,130	<0.005	0.8610			

Carapace length/width, plastron length/width and carapace length/weight functions have little application for field discrimination of sexes and there was no consistent difference in plastron curvature between sexes (Table 4). Most turtles had convex plastrons in longitudinal and transverse directions. The most useful external measurements for reliable identification of sex of at least some turtles were carapace length with tail length (Fig. 2E). While immature males and females may have similar tail lengths for the same SCL, most males with differentiated tails can be reliably distinguished from females. Similarly, the larger females can be distinguished reliably from males. However, Fig. 2E shows considerable overlap in the SCL/tail length distribution of immature males and of females (including immature and small adults).

Adult females were significantly larger than adult males for weight and measurements of carapace, plastron and head (Table 5). Adult males were significantly larger than adult females for all tail measurements. There is no 'knife-edge' minimum size that provided a 100% change from immaturity to adulthood for either sex. Rather, there was a wide size range over which there was a progressive change from 100% immature to 100% adult (Fig. 1B,C). This size range over which there was an increasing proportion of adults was different between the sexes. In comparing the results of logistic nonlinear and gompertz functions analyses of the proportion of adults at any size interval for each sex, it was found that the logistic nonlinear function provided the best fit to the results (Table 6, Fig. 3). Therefore, using the results of the logistic analysis, the size (\pm 95% confidence limits) at which 50% of the turtles were adults was:

for males, $AS_{50} = 18.89 \pm 0.081$ cm;

for females, $AS_{50} = 21.07 \pm 0.015$ cm.

These results provide an appropriate measure of the size at which these turtles attain sexual maturity.

During 26 December 1994 - 13 January 1995, 90% of adult female *E. krefftii* examined for breeding status ($n=20$) were breeding in that season: 12 had hard-shelled oviducal eggs and 1 had soft-shelled oviducal eggs. Of the remainder without oviducal eggs, 4 had mature follicles in the ovary, 1 had recently completed breeding for the season as indicated by large healing corpora lutea and atretic ovarian follicles ~4mm in diameter (13 January 1995), and 2 had not prepared for breeding in that breeding season as indicated by the largest ovarian follicles being <2mm in diameter and the absence of corpora lutea. For one of these two adult females not breeding in the 1994-1995 breeding season, the presence of corpora albicantia <1mm in diameter indicated that she had breed in a past breeding season. Some breeding females had both oviducal eggs and mature ovarian follicles ~12mm in diameter in late December indicating that they were laying multiple clutches within a breeding season. During July-August 1997, 98% of adult female *E. krefftii* examined ($n=54$) were in vitellogenesis with enlarging ovarian follicles in preparation for the next breeding season and none carried oviducal eggs. During 1-19 October 1996, while no turtles were examined internally to assess sex, maturity or breeding status, all short-tailed, adult sized turtles were palpated for oviducal eggs. No oviducal eggs were identified in any of these turtles.

During July-August 1997, 100% of adult male *E. krefftii* examined ($n=50$) were breeding for the year as indicated by each having a large pendulous epididymus with a distended white duct. In contrast, of the adult males whose gonads were examined in December ($n=5$: x4 in 1994, x1 in 1996), only 1 had a pendulous epididymus with a distended white duct. The remaining 4 had a pendulous epididymus with a non distended duct that was translucent in appearance. These latter adult males in December are interpreted as being between periods of active spermatogenesis. As a

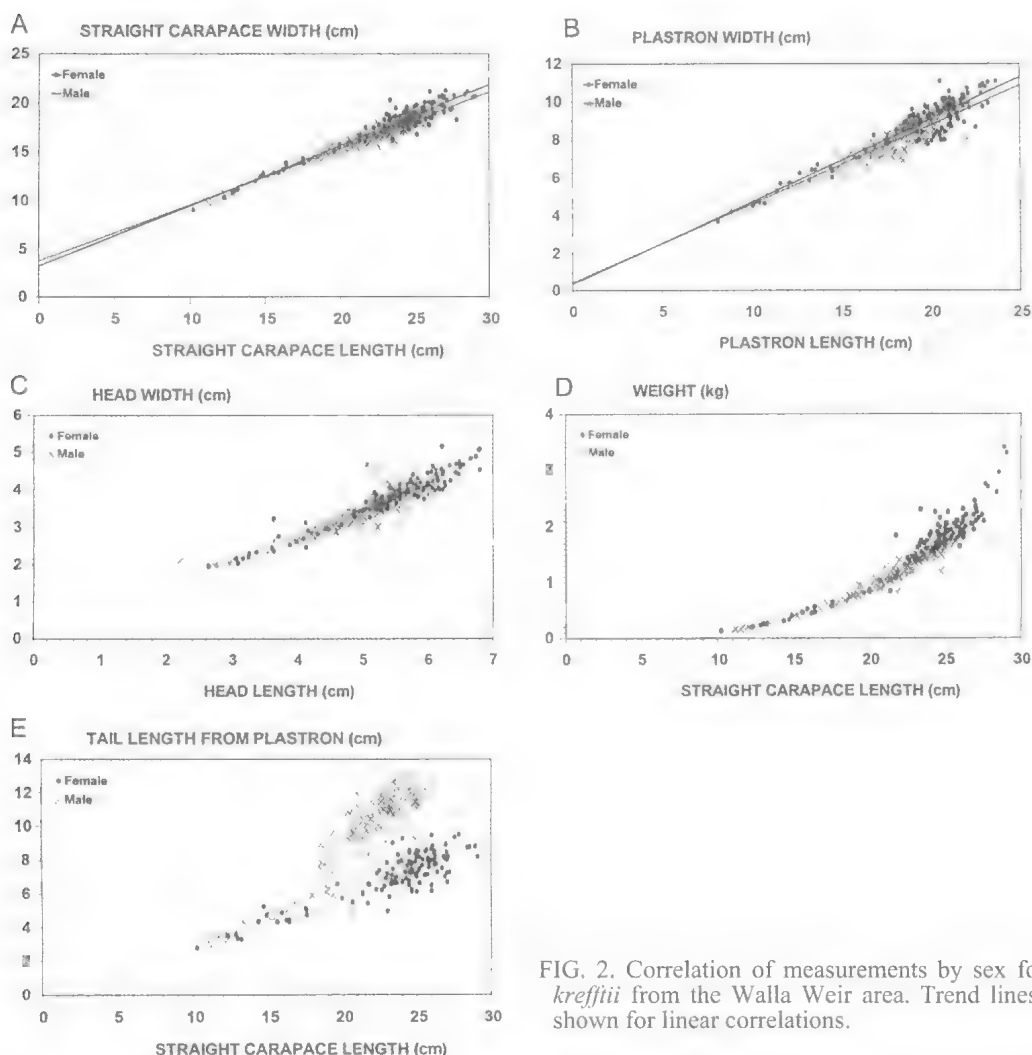


FIG. 2. Correlation of measurements by sex for *E. krefftii* from the Walla Weir area. Trend lines are shown for linear correlations.

result, the determination of the proportion of adult males breeding annually was restricted to the mid year sampling.

The breeding season has not been completely described for this population. Females with oviducal eggs were recorded during 26 December 1994 - 13 January 1995. One female laid eggs on 27 December 1994 as she was held for measurements. On 26 December 1994 there were some females with mature ovarian follicles that had yet to ovulate. While some females examined on 13 January 1995 were still in an egg production mode as judged by the presence of mature ovarian follicles that had not begun atresia, at least one female had completed its breeding season by that date (see above). These females lay eggs during a mid summer breeding

season without synchronised periods of ovulation and apparently without necessarily synchronised oviposition for the population. Some females are laying multiple clutches within a breeding season. The number of clutches per season and the number of eggs per clutch were not determined.

For the partial clutch of 5 eggs laid on 27 December 1994 (female tag number 13349; SCL = 25.75cm; Weight = 2.1kg): mean egg length = 3.58cm (SD = 0.153, range = 3.38-3.78); mean egg width = 2.13cm (SD = 0.153, range = 2.05-2.19); mean egg weight = 9.2g (SD = 0.261, range = 8.8-9.6). Two eggs hatched after an incubation period of 63 and 64 days, respectively. Mean hatchling measurements are summarised as follows:

TABLE 4. Frequency distribution of plastron curvature by sex and maturity for *E. krefftii* in the Walla Weir area. L denotes curvature along the length of the plastron. W denotes plastron curvature across the width of the plastron over the mid point.

Sex	Maturity	Plastron curvature								
		Convex L			Flat L			Concave L		
		Convex W	Flat W	Concave W	Convex W	Flat W	Concave W	Convex W	Flat W	Concave W
female	adult	81	2	0	0	0	0	1	0	0
female	immature	16	1	0	0	1	0	4	0	1
male	adult	68	0	0	4	2	0	9	0	4
male	immature	18	2	0	0	0	0	4	0	0

SCI=2.75cm (range=2.46-2.95); SCW=2.485cm (range=2.27-2.70); PL=2.315cm (range=2.13-2.50); PW=1.215cm (range=1.11-1.32); HL=1.11cm (range=1.10-1.12); HW=0.975cm (range=0.92-1.03); TLC=+0.61cm (range=0.58-0.64); TLP=0.78cm (range=0.71-0.85); TLV=0.485cm (range=0.44-0.53); WT=5.1g (n=1).

There were 6 short term recaptures of *E. krefftii* (1-23d; 2 adult female, 2 immature female, 1 adult male, 1 immature male) and all recaptures occurred within the original capture site. There were 5 long term recaptures from 4 *E. krefftii* (0.78-2.64yr; all adult females). Of these, 2 were recaptured in the same site (=displacements of no greater than a few hundred metres) and the remaining 3 recaptures involved movements exceeding 1km. Female 13364 moved ~1km upstream between 1 Jan 1995 - 23 Aug 1997. Female 13406 moved ~1km upstream between 1 Jan 1995 and 16 Oct 1996 and was recaptured ~0.5km downstream from the original capture site on 29 July 1997. The low proportion of recaptured turtles indicates either a very large population in the Walla Weir area or considerable movement of turtles within the river. Recorded displacements suggest home ranges greater than 1km of river. Considerably more recaptures are

needed to resolve questions concerning site fidelity and home range.

While most turtles were characterised by the standard scute count of 1 nuchal, 5 vertebrals, 4/4 costals and 12/12 marginals, 11.2% of *E. krefftii* had a non standard count (Table 7).

ELSEYA SP.

Elseya sp. was not abundant in any part of the river with 16 sightings for 14 captures of 13 turtles. It was recorded in only four small sections of the surveyed area. Eight captures were within <100m of one pool, immediately adjacent to the structural remains of the water uptake site for the old Wallaville Sugar Mill (study site 11). Almost all sightings (14/16) occurred from this site downstream for ~1km along this steep sided bend of the river (sites 11, 13 and 14). The remaining 2 sightings (including 1 capture) were at site 8. All capture sites were in 2-6m deep sections of the river with a steeply inclined underwater bank. All capture sites except site 8 were associated with large submerged rocks and snags. All were foraging or resting at the bottom of the stream when first encountered and there were no aquatic macrophytes growing at these locations.

TABLE 5. Measurements of *Emydura krefftii* from the Walla Weir area.

Measurement	Adult female				Adult male			
	mean	SD	range	n	mean	SD	range	n
Straight carapace length (cm)	25.10	1.557	21.73-29.10	96	22.90	1.717	18.56-27.83	66
Straight carapace width (cm)	18.82	1.068	16.20-21.24	96	16.97	1.074	14.48-19.14	66
Plastron length (cm)	20.63	1.244	18.06-23.69	96	18.45	1.276	14.78-21.84	65
Plastron width (cm)	9.46	0.742	7.91-11.09	96	8.41	0.694	6.56-10.05	64
Head length (cm)	5.76	0.464	4.85-6.80	96	5.14	0.436	4.05-6.05	64
Head width (cm)	4.05	0.405	3.27-5.16	96	3.55	0.382	2.79-4.55	64
Tail length from carapace (cm)	3.45	0.868	0.80-5.41	90	6.84	1.430	3.83-11.45	60
Tail length from plastron (cm)	7.61	0.895	4.96-9.51	90	10.79	1.276	7.85-13.25	60
Tail length from Vent (cm)	4.08	0.746	1.63-5.75	89	4.85	0.822	3.59-8.11	60
Weight (kg)	1.917	0.373	1.192-3.400	96	1.333	0.271	0.674-1.822	66

TABLE 6. Estimate of size at first breeding for *E. krefftii*: results of analysis of the ratio of adult to immature per 1cm size increments by sex for the data summarised in Fig. 3. A, Logistic function analysis; equation: proportion mature = $1 / (1 + \text{EXP}(-b * (\text{scl} - c)))$. B, Gompertz function analysis; equation: proportion mature = $\text{EXP}(-\text{EXP}(-b * (\text{scl} - c)))$.

A	Male			Female		
	value	Standard error	T-ratio	value	Standard error	t-ratio
Coefficient b	1.5535	0.28924	5.3710	2.5918	0.38949	6.6544
Coefficient c	18.885	0.040418	467.23	21.073	0.0076874	2741.2
Residual sum	-0.15122			-0.20340		
Residual variance	0.0049432			0.0013822		
Log-likelihood function	11.12341			14.98493		
df	7			6		
B	Male			Female		
	value	Standard error	T-ratio	value	Standard error	t-ratio
Coefficient b	9.8502	0.99828	9.8671	8.2830	1.1757	7.0449
Coefficient c	19.889	0.096949	205.15	20.989	2.0089	10.448
Residual sum	0.74704			-0.17702		
Residual variance	0.052084			0.0026914		
Log-likelihood function	0.5265644			12.31928		
df	7			6		

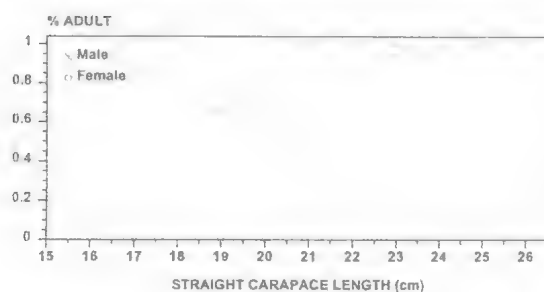


FIG. 3. Calculation of AS_{50} values for female and male *E. krefftii* from the Walla Weir area.

Laparoscopic examination of the cloaca showed two large sac-like structures (=cloacal bursae) leading anteriorly from the cloaca to lie within the posterior body cavity. During laparoscopic examination of the gonads, these bursae were visible in the body cavity and were positioned one either side of the bladder. The posterior portion of each bursa was crowded with numerous thin-walled, branched but flattened processes, each well supplied with blood vessels. Muscular action of the bursae flushed water, via the vent, in and out of the sacs and past the vascularised processes. In contrast, *E. krefftii* observed in a similar manner had much smaller cloacal bursae with only relatively small areas of branched processes. The large cloacal bursae and associated vascularised processes of *Elseya* sp.

resemble the cloacal gill systems of *Rheodytes leukops* (Legler & Cann, 1980) and *E. georgesi* (= *E. latisternum* of King & Heatwole, 1994a).

The 13 *Elseya* sp. ranged from small immature turtles with $SCL=11.48$ cm to large adults with $SCL=38.8$ cm. The sample contained 6 females (4 adult, 2 immature), 4 males (2 adult, 2 immature) and 3 unsexed immature turtles. The size class distribution by sex of captured *Elseya* sp. is summarised in Fig. 4. A summary of the size by weight distribution is shown in Fig. 5. The size and weights of adult male and female *Elseya* sp. from the Walla Weir area are summarised in Table 8. Within this small sample, the adult females were much larger than the adult males except that adult males had longer tails than females. It was not possible to quantify AS_{50} values from this sample.

The small sample limits definition of the breeding season in this part of the Burnett R. The 3 adult females captured in July 1997 were in early vitellogenesis in preparation for the next breeding season and each also had healing corpora lutea on their ovaries resulting from a breeding season earlier in the year. The 2 adult females captured in early January 1995 were in advanced vitellogenesis for an approaching nesting season and neither had corpora lutea on the ovaries. None from either sample contained oviducal eggs. These observations are consistent with oviposition occurring during approximately

TABLE 7. Frequency distribution of scute counts for chelid turtles from the Walla Weir area. For paired scutes, the left side was counted first.

Scute	Scute count	Frequency			
		<i>Emydura krefftii</i>	<i>Elseya</i> sp.	<i>Elseya latisternum</i>	<i>Chelodina expansa</i>
nuchal	0	10	12	2	4
	1	276	1	0	0
vertebral	5	285	12	2	0
	6	1	0	0	2
	7	0	1	0	2
costals	3/3	0	0	0	1
	4/3	1	0	0	0
	4/4	275	11	2	2
	4/5	1	1	0	0
	5/4	8	0	0	0
	5/5	1	0	0	0
	5/6	0	1	0	1
marginals	11/10	1	0	0	0
	11/12	1	0	1	0
	11/13	2	0	0	0
	12/11	2	0	0	1
	12/12	271	13	1	3
	12/13	3	0	0	0
	13/12	4	0	0	0
	13/13	2	0	0	0

autumn or early winter. For the 5 captures of 4 adult females, all were in vitellogenesis. This indicates that the annual breeding rate of adult females may approach 100%. Both adult males captured in late July 1997 were in active sperm production for the next breeding season as indicated by an enlarged white duct within the pendulous epididymus.

The 5 immature *Elseya* sp. captured in December 1994-January 1995 each had 5 growth layers not including the hatchling layer on several scutes. These indicated that they were part of a single year cohort born in 1990. The immature specimen captured in July 1997 had 6 growth layers not including the hatchling layer on several scutes indicating birth in 1991.

The single recapture was of an adult female, tag 13408, originally tagged on 1 Jan 1995 (SCL=37.9cm, 6.85kg). She was recaptured within 10m of her original capture site on 29 Jul 1997 (2.58yr at large and two wet seasons of floods between captures). She had grown 0.9cm in SCL (growth rate = 0.34cm/yr) and lost 0.35kg in weight between captures.

While most turtles were characterised by the standard scute count of 0 nuchal, 5 vertebrales, 4/4 costals and 12/12 marginals, 23% of *Elseya* sp. had a non standard count (Table 6).

ELSEYA LATISTERNUM

Only 2 specimens were recorded (immature male, SCL=16.12cm, weight=0.468kg; adult female, SCL=22.46cm, weight=1.57cm). Both were captured in larger pools 2-6m deep. The adult female (13869) was classed as an adult that had yet to breed. It had no corpora albicantia and no corpora lutea in the ovaries, but small vitellogenic follicles and atretic disks ~2mm in diameter resulting from past atresia of enlarged vitellogenic follicles. This female had entered a past vitellogenic cycle, but had not ovulated. This is not necessarily indicative of an environmental problem as failure to breed on the first vitellogenic cycle has been recorded as normal for young adult females of other chelid species (Kuchling & Bradshaw, 1993) and marine turtles (Limpus, 1990). The immature male was recaptured within the same site 4d after its original capture. Scute counts for *E. latisternum* are summarised in Table 7.

E. latisternum is usually more abundant in the upper reaches of streams in more elevated areas (CJL, unpublished data) and the Walla Weir area of the Burnett R. is considered marginal to its normal distribution in this river.

CHELODINA EXPANSA

During the entire study, only 5 specimens were captured in the river and another was recovered as a carcass on the bank. They ranged from immature turtles (SCL=15.74cm) to adults (SCL=29.05cm). For scute counts see Table 7.

DISCUSSION

This baseline study of freshwater turtles in the Walla Weir area of the Burnett R. has shown *Elseya* sp. to be an uncommon species for the

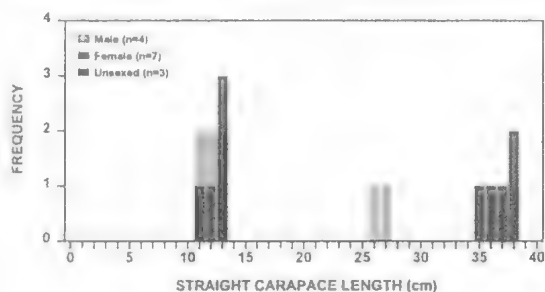


FIG. 4. Frequency distribution by size and sex for *Elseya* sp. from the Walla Weir area.

TABLE 8. Measurements of adult *Elseya* sp. from the Walla Weir area.

Measurement	Adult female				Adult male			
	mean	SD	range	n	mean	SD	range	n
Straight carapace length (cm)	37.42	1.16	35.6-38.8	5	27.27	0.33	26.94-27.6	2
Straight carapace width (cm)	29.83	0.61	28.95-30.65	5	21.86	0.04	21.82-21.90	2
Plastron length (cm)	30.92	0.46	30.53-31.82	5	21.89	0.05	21.84-21.94	2
Plastron width (cm)	14.41	0.79	13.51-15.76	5	10.10	0.21	9.89-10.31	2
Head length (cm)	9.65	0.64	8.52-10.33	5	7.19	0.25	6.94-7.44	2
Head width (cm)	6.87	0.28	6.66-7.40	5	4.98	0.19	4.79-5.16	2
Tail length from carapace (cm)	3.01	0.77	2.02-4.39	5	8.00	0.53	7.47-8.52	2
Tail length from plastron (cm)	10.13	0.82	9.44-11.73	5	14.64	0.06	14.58-14.69	2
Tail length from vent (cm)	6.97	0.77	6.08-8.34	5	7.32	0.14	7.18-7.45	2
Weight (kg)	6.62	0.19	6.35-6.85	5	2.17	0.03	2.15-2.20	2

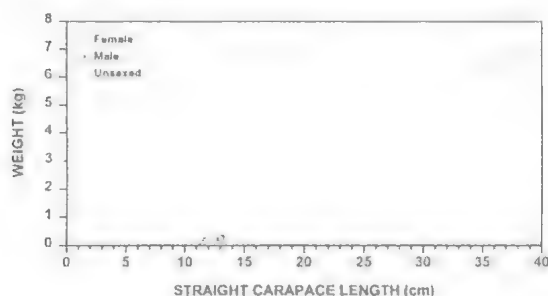
area. A small area adjacent to the site of the old Wallaville Sugar Mill has been identified where the majority of specimens were concentrated. The population in 1994-1997 consisted of a few large adults and a small cohort(s) of immature turtles born in about 1990-91. This population structure suggests that the species was not functioning well during the study period. The reasons for this current population structure could not be assessed within the short time frame of this baseline study developed since the presentation of the Boardman (1996) review and required to be completed before water levels rose with the construction of the Walla Weir in late 1997. The identification of a cloacal gill system in *Elseya* sp. resembling the cloacal gills of species with aquatic respiration such as *Elseya georgesi* (King & Heatwole, 1994a,b) and *Rheodytes leukops* (Priest, 1997) indicated that the diving physiology of *Elseya* sp. warranted investigation. Such a study has commenced and *Elseya* sp. from the Mary R. has been found to have a very well-developed capacity for aquatic ventilation (FitzGibbon, 1998). However, the impact of impoundment with lowered dissolved

oxygen concentrations on life history parameters for this species remains unresolved.

An adequate set of statistically described parameters suitable for assessment of temporal changes in the dynamics of a freshwater turtle population requires a sample of some hundreds of individuals of the species being examined. It is now apparent that it was not logistically possible to capture a sample of hundreds of *Elseya* sp. from the Walla Weir area of the Burnett R. within a short period. Any assessment of temporal change for *Elseya* sp. within the Walla Weir following elevation of water level within the impoundment must be made in comparison with the performance of the much more abundant species *E. krefftii* within the Walla Weir and with *Elseya* sp. populations elsewhere.

Examination of the large sample of *E. krefftii* during the baseline study has provided data that, on comparison with a comparable data set following elevation of water levels in the impoundment, should enable temporal changes in population function to be assessed within the area. These parameters include size class distribution by sex, size class distribution by maturity for each sex, estimation of the size for first breeding (AS_{50}) for each sex, mean size of breeding adults for each sex, annual breeding rate for adults of each sex and length/weight condition curves for each sex. These types of parameters can be measured during short term studies independent of long term mark-recapture studies.

Accurate recording of data that includes sex, maturity and breeding status of freshwater turtles usually requires the examination of the gonads and associated ducts. The present study has demonstrated that external measurements do not provide knife-edge delineation of either sex or

FIG. 5. Distribution of the size by weight of *Elseya* sp. from the Walla Weir area.

maturity and they provide no clear indication of breeding condition. Breeding adult females can be identified by palpation of soft-shelled and hard-shelled oviducal eggs. Conservation ethics preclude the killing of large series of turtles to obtain reproductive data. Therefore, assessing sex, maturity and breeding status of live turtles requires alternative methods. In this context, radiography is limited to identifying the presence of and counts of shelled oviducal eggs and hence identifying gravid females (Kuchling, 1998). However, when considering health hazards, Kuchling (1998) has urged caution in using radiography for routine screening of turtle populations to obtain reproductive data. In contrast, the benign technique of ultrasound scanning can provide detailed images for most stages of the female reproductive cycle including vitellogenic and atretic follicles in the ovaries and freshly ovulated ova, and soft-shelled and hard-shelled oviducal eggs in the oviducts (Kuchling, 1998). Unfortunately, ultrasound scanning does not provide resolution of soft bodied organs such as oviduct, testis and epididymus (CJL unpublished data). Ultrasound scanning is, therefore, limited in application for determining the sex of small turtles, for determining the change from immature to mature in males and early adult females, and for determining presence or absence of spermatogenesis of adult males. Examination via laparoscopy provides for direct visual inspection of the gonads and associated ducts with a high degree of visual resolution and has been used extensively in population dynamics studies of marine turtles (Limpus & Reed, 1985; Limpus, 1992; Limpus et al., 1994a,b), terrestrial turtles (Robeck et al., 1990; Rostal et al., 1994) tuatara (Cree et al., 1991) and crocodiles (Limpus, 1984). Use of laparoscopic examination in the present study demonstrates the wide range of reproductive parameters that can be obtained from a sample that includes a wide cross-section of sizes of a population. As with any surgical procedure there may be a health risk to the 'patients', but this risk can be minimised to <0.2% mortality through adequate surgical training in the use of the equipment, in depth knowledge of turtle anatomy and use of field surgical procedures that approach sterile conditions.

With long-lived species such as freshwater turtles (Parmenter, 1985; Gibbons, 1989; Kennett, 1994), adult turtles can be plentiful in a population for a very long time, even if hatchling recruitment is severely compromised (Thomson, 1983; Congdon et al., 1993). A significant

limitation on clarifying population dynamics for Australian freshwater turtle populations is the current lack of a reliable technique for determining the age of live turtles. Addition of age to the suite of variables measured would significantly improve the capacity to identify change in population dynamics. If changes are detected within a turtle population at a site like the Walla Weir, it is unlikely that the underlying causes of change can be identified in the absence of comprehensive long term studies. Comprehensive demographic and ecological data is available for only one species of Australian freshwater turtle — the endangered *P. umbrina* from southwestern Australia (Kuchling & Bradshaw, 1993; Kuchling et al., 1992). Similar data for Queensland freshwater turtle species would benefit management planning for conservation.

The paucity of small immature turtles in the *E. krefftii* population and the limited size class representation in the *Elseya* sp. population at Walla Weir is reminiscent of the stressed populations of *E. macquarii* and *C. longicollis* in the Murray R. where predation of eggs was identified as a significant problem limiting hatchling recruitment (Thomson, 1983). This latter study indicates the need to address more than in-river problems with freshwater turtle conservation issues.

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LITERATURE CITED

- BOARDMAN, N.K. 1996. Independent review of impacts of Walla Weir proposal on lungfish (*Neoceratodus forsteri*) and *Elseya* tortoise. Unpublished report to the Federal Minister of the Environment, 5 August 1996. 17p.
- CANN, J. 1998. Australian Freshwater Turtles. (Beaumont Publishing: Singapore.)
- CREE, A., COCKREM, J.F., BROW, M.A., WATSON, P.R., GUILLETTE, L.J., NEWMAN, P.G. & CHAMBERS, G.K. 1991. Laparoscopy, radiography and blood analysis as techniques for identifying reproductive conditions of female Tuatara. *Herpetologica* 47: 238-249.
- CONGDON, J.D., DUNHAM, A.E. & VAN LOBEN SELS, R.C. 1993. Delayed sexual maturity and

- demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. *Conservation Biology* 7: 826-833.
- FITZGIBBON, S. The diving physiology and dive behaviour of an undescribed turtle from the Mary River, Queensland (*Elseya* sp.). Unpublished B.Sc.(Hons.) thesis, Zoology Department, University of Queensland, Brisbane.
- GEORGES, A. 1994. Setting conservation priorities for Australian freshwater turtles. Pp. 453-76. In Lunney, D. & Ayers, D. (eds) *Herpetology in Australia: a diverse discipline*. (Royal Zoological Society of New South Wales: Mosman).
- GEORGES, A. & ADAMS, M. 1992. A phylogeny for Australian chelid turtles based on allozyme electrophoresis. *Australian Journal of Zoology* 40: 453-476.
1996. Electrophoretic deliniation of species boundaries within the short-necked freshwater turtles of Australia. *Zoological Journal of the Linnean Society* 118: 241-260.
- GIBBONS, J.W. 1989. Life history and ecology of the slider turtle. (Smithsonian Institution Press: Washington, D.C.).
- KENNETT, R. 1994. Ecology of two species of freshwater turtle, *Chelodina rugosa* and *Elseya dentata*, from the wet-dry tropics of northern Australia. Unpublished PhD thesis. University of Queensland, Darwin.
- KENNETT, R.M. & GEORGES, A. 1990. Habitat utilisation and its relationship to growth and reproduction of the eastern long-necked turtle, *Chelodina longicollis* (Testudinata: Chelidae), from Australia. *Herpetologica* 46: 22-33.
- KING, P. & HEATWOLE, H. 1994a. Non-pulmonary respiratory surfaces of the chelid turtle *Elseya latisternum*. *Herpetologica* 50: 262-265.
- 1994b. Partitioning of aquatic oxygen uptake among different respiratory surfaces in a freely diving pleurodiran turtle, *Elseya latisternum*. *Copeia* 1994: 802-806.
- KUCHLING, G. 1998. How to minimise risk and optimise information gain in assessing reproductive condition and fecundity in live female chelonians. *Chelonian Conservation and Biology* 3: 118-123.
- KUCHLING, G. & BRADSHAW, S.D. 1993. Ovarian cycle and egg production of the western swamp tortoise *Pseudemydura umbrina* (Testudines: Chelidae) in the wild and in captivity. *London Journal of Zoology* 229: 405-419.
- KUCHLING, G., DEJOSE, J.P. & BURBIDGE, A.A. 1992. Beyond captive breeding: the western swamp tortoise *Pseudemydura umbrina* recovery program. *International Zoo Yearbook* 31: 37-41.
- LEGLER, J.M. & CANN, J. 1980. A new genus and species of chelid turtle from Queensland, Australia. *Natural History Museum of Los Angeles County Contributions in Science* 324: 1-18.
- LIMPUS, C.J. 1984. Identification of ovarian follicles and oviducal eggs by cloacal examination of live Australian freshwater crocodiles. *Australian Wildlife Research* 11: 203-204.
1990. Puberty and first breeding in *Caretta caretta*. National Oceanic and Atmospheric Administration Technical Memorandum National Marine Fisheries Service -Southeast Fisheries Science Center 278: 81-83.
1992. The hawksbill turtle, *Eretmochelys imbricata*, in Queensland: population structure within a southern Great Barrier Reef feeding ground. *Wildlife Research* 19: 489-506.
- LIMPUS, C.J. & REED, P.C. 1985. The green turtle, *Chelonia mydas*, in Queensland: a preliminary description of the population structure in a coral reef feeding ground. Pp.47-52. In Grigg, G., Shine, R. & Ehmann, H (eds) *Biology of Australasian Frogs and Reptiles*. (Surrey Beatty & Sons: Chipping Norton).
- LIMPUS, C.J., COUPER, P.J. & READ, M.A. 1994a. The loggerhead turtle, *Caretta caretta*, in Queensland: population structure in a warm temperate feeding area. *Memoirs of the Queensland Museum* 37: 195-204.
- 1994b. The green turtle, *Chelonia mydas*, in Queensland: population structure in a warm temperate feeding area. *Memoirs of the Queensland Museum* 35: 139-154.
- MANNING, B. & KOFRON, C.P. 1996. Evolution and Zoogeography of Australian freshwater turtles. *Memoirs of the Queensland Museum* 39: 319-331.
- PARMENTER, C.J. 1985. Reproduction and survivorship of *Chelodina longicollis* (Testudinata: Chelidae). Pp. 54-61. In Grigg, G., Shine, R. & Ehmann, H (eds) *Biology of Australasian Frogs and Reptiles*. (Surrey Beatty & Sons: Chipping Norton).
- PRIEST, T. 1997. Bimodal respiration and dive behaviour of the Fitzroy River Turtle, *Rheodytes leukops*. Unpublished B.Sc. Honours thesis, Zoology Department, University of Queensland, Brisbane.
- PRITCHARD, P.C.H. & TREBBAU, P. 1984. The turtles of Venezuela. (Society for the Study of Amphibians and Reptiles: Athens, USA).
- ROBECK, T.R., ROSTAL, D.C., BURCHFIELD, P.M., OWENS, D.W. & KRAEMER, D.C. 1990. Ultrasound imaging of reproductive organs and eggs in Galapagos tortoises, *Geochelone elephantopus* spp. *Zoo Biology* 9: 349-359.
- ROSTAL, D.C., GRUMBLES, J.S., LANCE, V.A. & SPOTILA, J.R. 1994. Non lethal sexing techniques for hatchling and immature desert tortoises (*Gopherus agassizii*). *Herpetological Monograph* 8: 83-87.
- THOMSON, M.B. 1983. Populations of the Murray River tortoise, *Emydura* (Chelodina): the effect of egg predation by the red fox, *Vulpes vulpes*. *Australian Wildlife Research* 10: 363-371.

A NEW EURYLEPTID FLATWORM (PLATYHELMINTHES, POLYCLADIDA) ASSOCIATED WITH A COLONIAL ASCIDIAN FROM THE GREAT BARRIER REEF

LESLIE J. NEWMAN

Newman, L.J. 2002 5 31: A new euryleptid flatworm (Platyhelminthes, Polycladida) associated with a colonial ascidian from the Great Barrier Reef. *Memoirs of the Queensland Museum* 48(1): 169-1672 Brisbane. ISSN 0079-8835.

A new polyclad flatworm, *Ascidiophilla alba* gen. et sp. nov. (Platyhelminthes, Polycladida) is described from Lizard Island, north Queensland. This new species was found to be closely associated with the colonial ascidian, *Didemnum molle* (Herdman, 1886). Animals were observed crawling out of their host at night. This new genus possesses characters of both euryleptids (tubular pharynx) and pseudocerotids (single horseshoe-shaped cerebral eye cluster and short pseudotentacles with dorsal and ventral eyes). □ *Polycladida*, *Euryleptidae*, flatworm, symbiosis, ascidian, taxonomy.

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Recent studies on polyclad flatworms have shown that the pseudocerotids are by far the most conspicuous and diverse family of turbellarians inhabiting coral reefs (Newman & Cannon, 1994a, b, 1995a, 1996a, b, 1997, 1998). However, little is known about the equally diverse and closely related Euryleptidae members of which are often as brilliantly coloured as the pseudocerotids (Newman & Cannon, 2000; Newman et al., 2000).

As with most polyclads, these delicate worms tend to fall apart on fixation so that animals have rarely been properly fixed for histological preparations or taxonomic studies and as a consequence type material is often lacking. Few studies have dealt with living animals and thus many morphological features have not been examined.

According to Prudhoe (1985), polyclads are well known commensals of a variety of invertebrates including bivalves, crabs and shrimps, sea urchins, nemerteans and corals. However, there are only a handful of reports on biology of the cotyleans. Newman & Cannon (1994b) noted that *Pseudoceros bifurcus* Prudhoe, 1989 was found with and fed on a variety of ascidian species. Furthermore, Crozier (1917) and Newman et al. (2000) showed that the euryleptid, *Maritigrella crozieri* (Hyman, 1939) lived exclusively on the mangrove ascidian, *Ecteinascidia turbinata* Herdman, 1880 and soon died without its host.

A new monotypic genus is described here from Lizard Island, northern Great Barrier Reef. Animals were found to be closely associated with

the colonial ascidian, *Didemnum molle*, Herdman, 1886.

METHODS

Animals were hand collected on scuba at night from colonies of *D. molle*, Lizard Island Lagoon, northern Great Barrier Reef, Queensland. Worms were photographed in situ, fixed on frozen polyclad fixative (Newman & Cannon, 1995b) and preserved in 70% ethanol for histological preparations. Whole mounts were stained with Mayer's haemalum, dehydrated in graded alcohols and then mounted in Canada balsam. Longitudinal serial sections of the reproductive region were obtained from specimens embedded in Paraplast (56°C), sectioned at 5–7 µm, and then stained with haematoxylin and eosin.

Measurements (mm) of the body were taken from live animals in a relaxed state and are given as length × width. Measurements of the reproductive organs are taken from the paratypes. Reconstruction of the reproductive system is diagrammatic and derived from the sections with minimal interpretation. Drawings were made with the aid of a camera lucida. Material is lodged at the Queensland Museum (QM) as whole mounts (WM), serial sections (LS) and wet specimens (S).

Family EURYLEPTIDAE Stimpson, 1857

Ascidiophilla gen. nov.
(Figs 1,2)

ETYMOLOGY. *Ascidio*: ascidian and *philla*: loving, (L fem.) for its close association with *D. molle*.

DIAGNOSIS. Emended from Cannon (1986). Euryleptidae with papillate dorsal surface, small folded pseudotentacles, cerebral eyes in a single loose horseshoe-shaped cluster, dorsal and ventral tentacular eyes present. Pharynx tubular and mouth anterior. Copulatory complex behind the pharynx, lying posteriorly to the male pore, penis papilla with a short pointed stylet.

TAXONOMIC REMARKS. The position of this genus is precarious as it shows characteristics of the Pseudocerotidae (simple folded pseudotentacles and a single horseshoe-shaped cerebral eyespot) and the Euryleptidae (tubular pharynx). However, it is placed in the Euryleptidae due to systematic importance of a tubular pharynx as suggested by Faubel (1984) and Cannon (1986).

The Euryleptidae is relatively large with about 14 genera. The majority possess a smooth dorsal surface. According to Faubel (1984) only *Cycloporus* Lang 1884 possesses a 'knobbed' dorsal surface. However, *Cycloporus* lack tentacles, the cerebral eyes are in two elongate clusters and these flatworms possess distinct peripheral vesicles that open to the exterior (Faubel, 1984; Prudhoe, 1985). In comparison, *Ascidiophilla* gen. nov. has distinct folded pseudotentacles, the cerebral eyespots are in a single horseshoe-shaped cluster and there are no peripheral vesicles.

***Ascidiophilla alba* sp. nov.**

ETYMOLOGY. Latin *alba*, white for its distinctive colour.

MATERIAL. HOLOTYPE. Lizard Island Lagoon, northern Great Barrier Reef (GBR), 2m depth, night, collected from *Didemnum molle*, 10 April 1995, L. Newman and A. Flowers, WM QMG211065. **PARATYPES.** Same data, S, QMG211181; same data, 7 April, 1995; LS, QMG211075; same data, 10 April, 1995, C. & H. Peterken, LS (QMG211064); same data; WM, QMG211182, same data.

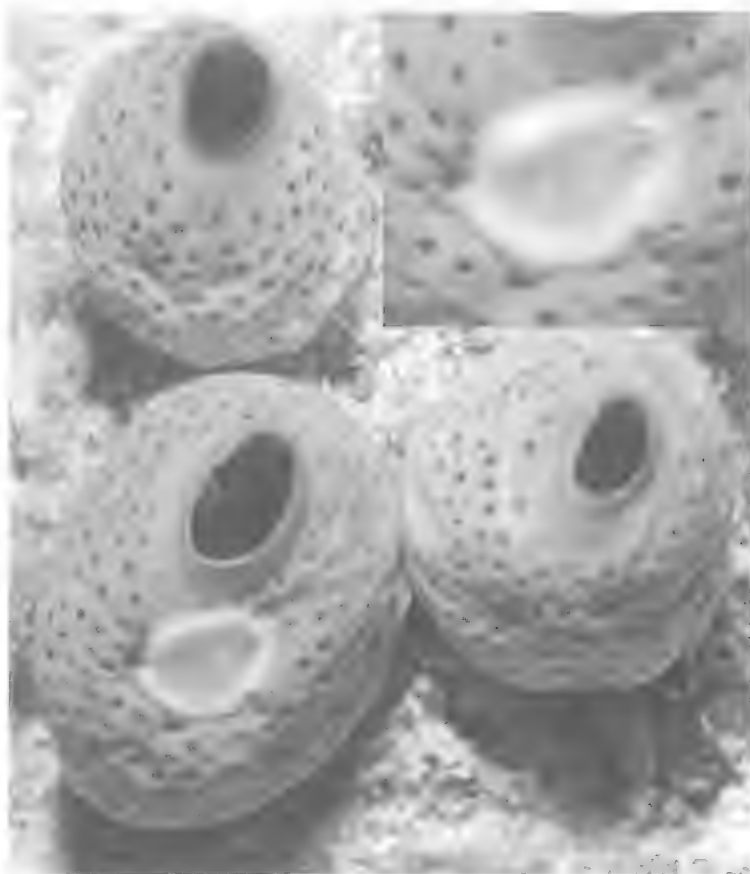


FIG. 1. Colonial ascidian *Didemnum molle* with the flatworm *Ascidiophilla alba* gen. et sp. nov., at night, Lizard Island Lagoon, northern Great Barrier Reef, Australia; insert showing close-up of the flatworm (80 × mag.). (photo A. Flowers & L. Newman)

DIAGNOSIS. Small, round, white with red dots on the margin.

DESCRIPTION. Dorsal and ventral surfaces semi-transparent, mottled opaque and transparent white. Dorsal margin opaque with small red dots. Entire dorsal surface covered with about 20 short rounded papillae, cerebral eyespot in light orange-brown area (Fig. 1).

Body small, round, without marginal ruffling (Figs 1, 2A). Marginal tentacles appear as short, folded, pseudotentacles with 6-10 eyes in two scattered clusters (Fig. 2A-C). Cerebral eyespot with a single loose horseshoe shaped cluster of 10-30 eyes (Fig. 2B, C). Dorsal tentacular eyes in scattered clusters of about 6 eyes each, ventral marginal eyes in loose clusters with 5-10 eyes each. Pharynx small, anterior and tubular (Fig.

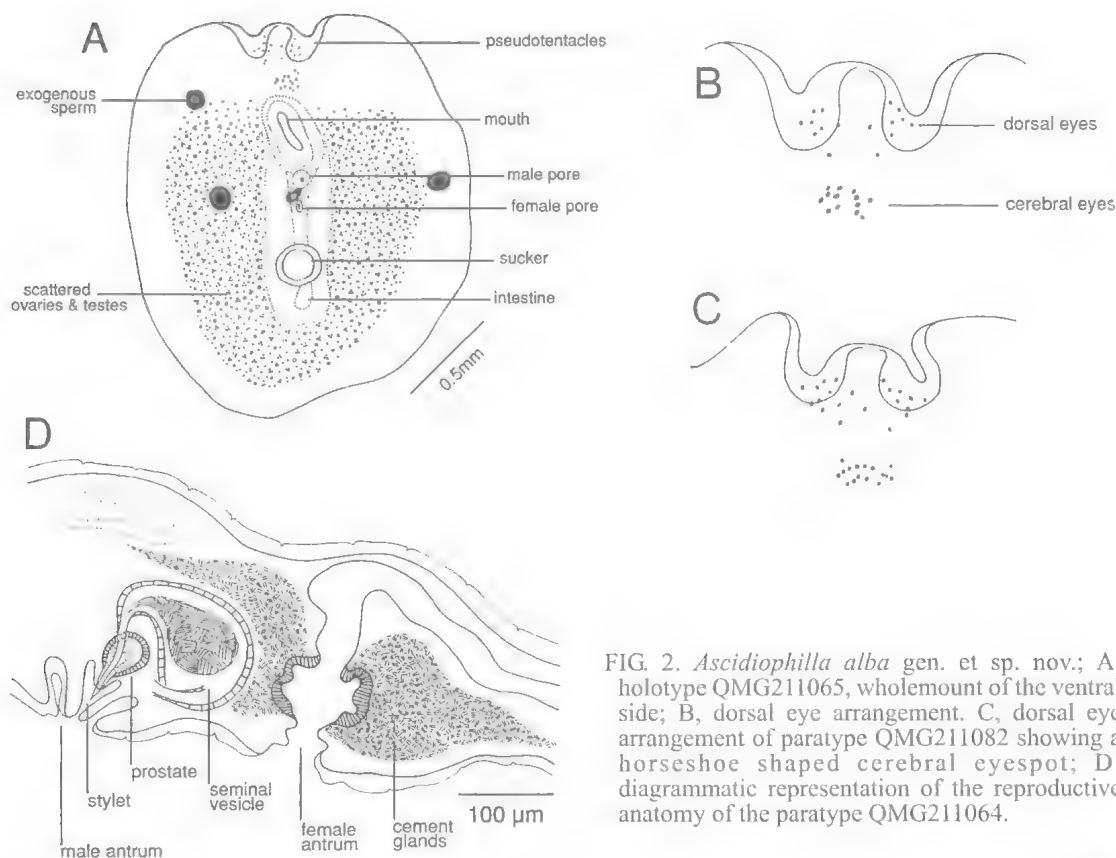


FIG. 2. *Ascidiophilla alba* gen. et sp. nov.; A, holotype QMG211065, wholemount of the ventral side; B, dorsal eye arrangement. C, dorsal eye arrangement of paratype QMG211082 showing a horseshoe shaped cerebral eyespot; D, diagrammatic representation of the reproductive anatomy of the paratype QMG211064.

2A). Sucker large, posterior to the midline. Pseudotentacle terminals held erect when alive (Fig. 1).

Genopores anterior to the midline, posterior to the pharynx (Fig. 2A). Male pore small, anterior and well separated from the female pore (Fig. 2A, D). Male antrum wide and deep. Prostate rounded oval (55µm long), seminal vesicle rounded oval (170µm long) with thin walls, prostatic duct and ejaculatory ducts straight, not joining and leading separately into the penis papilla. Stylet extremely small (18µm long) and pointed. Female antrum deep and wide with extensive cement glands. Vagina leads dorsally and posteriorly. Size range 4 × 2mm to 5 × 3mm, all mature.

HABITAT AND DISTRIBUTION. Animals were initially observed on the outside of colonies of *D. molle* at night. Specimens of *D. molle* were brought back to the laboratory and worms were observed to crawl out of common atrial opening of individual colonies only at night. No worms were observed on the ascidians during the day

either in situ or in the laboratory. Several other species of colonial ascidians retained in the laboratory did not yield flatworms nor would these polyclads retreat into any other ascidian species that was offered. The species is known only from Lizard Island Lagoon, northern Great Barrier Reef.

DISCUSSION. Unlike the pseudocerotids, Newman & Cannon (1994a) noted that euryleptids were relatively rare in Great Barrier Reef waters. However, according to Prudhoe (1985) this family appears to be restricted to cooler waters. On the other hand, Newman et al. (2000) noted that the most common species within warm southwest Atlantic waters was the euryleptid *Maritigrella crozieri*. It appears that there are too few reports on these elusive flatworms to make distributional generalisations.

Members of the euryleptid *Maritigrella* were observed feeding on solitary or colonial ascidians during the day and displayed disruptive colour patterns of transverse stripes and spots (Newman & Cannon, 2000; Newman et al., 2000).

Conversely, *Ascidiophilla* gen. nov. was inconspicuously drab. Perhaps its lack of colour or pattern is due to its nocturnal nature since it would not necessarily need to advertise warning colours during the day to visual predators like so many other polyclads (Ang & Newman, 1998).

Ascidiophilla gen. nov. appears to live within the common atrial cavity of *D. molle* colonies. It is not known whether or not it consumes the whole ascidian colony. In the absence of data to the contrary, it is assumed that this is a commensal relationship in which the worm gains protection from sheltering in the ascidian colony.

Newman et al. (2000) noted that *M. crozieri* contained the same cytotoxic substances known to occur within its prey, *E. turbinata*. These substances were tested in pre-clinical trials as anticancer agents (Carté, 1996). Hence, it is important to not only document the biodiversity of these turbellarians but to also understand their feeding biology.

Systematics of the Euryleptidae remains problematic as taxonomic studies are scarce and type material is scattered or lacking. This study highlights the need for further studies on living animals, use to photography and feeding observations.

ACKNOWLEDGEMENTS

I thank Andrew Flowers and Hugh and Carolyn Peterken for their assistance collecting and photographing these worms. Specimens were prepared for histology by Zeinab Khalil and curated by Mal Bryant and Kim Sewell. Financial support was generously provided by the Australian Biological Resource Study, Canberra. I would also like to thank Lyle Vale and Anne Hoggett, Directors of the Lizard Island Research Station; the Queensland Museum, Brisbane; and the School of Environmental Science and Management, Southern Cross University.

LITERATURE CITED

- ANG, H.P. & NEWMAN, L.J. 1998. Warning colouration in pseudocerotid flatworms (Platyhelminthes, Polycladida). A preliminary study. *Hydrobiologia* 383: 29-33.
- CANNON, L.R.G. 1986. *Turbellaria of the World – a guide to families and genera*. (Queensland Museum: Brisbane).
- CARTÉ, B.K. 1996. Biomedical potential of marine natural products. *Bioscience* 46: 271-286.
- CROZIER, W.J. 1917. On the pigmentation of a polyclad. *Proceedings of the American Academy of Arts and Sciences* 52: 723-730.
- FAUBEL, A., 1984. The Polycladida, Turbellaria. Proposal and establishment of a new system. Part II. The Cotylea. *Mitteilungen aus dem hamburgischen zoologischen Museum und Institut* 8: 189-259.
- NEWMAN, L.J. & CANNON, L.R.G. 1994a. Biodiversity of Australian polyclad flatworms. *Memoirs of the Queensland Museum* 36: 159-163.
- 1994b. *Pseudoceros* and *Pseudobiceros* (Polycladida, Pseudocerotidae) from Eastern Australia and Papua New Guinea. *Memoirs of the Queensland Museum* 37: 205-266.
- 1995a. Colour variation in *Pseudoceros* (Platyhelminthes, Polycladida). *The Raffles Bulletin of Zoology* 43: 435-446.
- 1995b. The importance of the fixation of colour, pattern and form in tropical Pseudocerotidae (Platyhelminthes, Polycladida). *Hydrobiologia* 305: 141-143.
- 1996a. New pseudocerotid genera (Platyhelminthes, Polycladida) from Australasian coral reefs. *Journal of Natural History* 30: 1425-1441.
- 1996b. *Bulaceros*, new genus and *Tytthosoceros*, new genus (Platyhelminthes, Polycladida, Pseudocerotidae) from the Great Barrier Reef, Australia and eastern Papua New Guinea. *Raffles Bulletin of Zoology* 44: 479-492.
1997. Nine new *Pseudobiceros* (Platyhelminthes, Polycladida, Pseudocerotidae) from the Indo-Pacific. *Raffles Bulletin of Zoology* 45: 341-368.
1998. New *Pseudoceros* (Platyhelminthes, Polycladida, Pseudocerotidae) from the Indo-Pacific. *Raffles Bulletin of Zoology* 46: 293-323.
2000. A new genus of euryleptid flatworm (Platyhelminthes, Polycladida, Euryleptidae) from the Indo-Pacific. *Journal of Natural History* 34: 191-205.
- NEWMAN, L.J., NORENBURG, J.L. & REED, S. 2000. Taxonomic and biological observations on the tiger flatworm, *Maritigrella crozieri* (Hyman, 1939), new combination (Platyhelminthes, Polycladida, Euryleptidae) from Florida waters. *Journal of Natural History* 34: 799-808.
- PRUDHOE, S. 1985. *A monograph on Polyclad Turbellaria*. (Oxford University Press: Oxford).

CATALOGUE OF METEORITES, TEKTITES AND ASSOCIATED MATERIAL FROM THE UNIVERSITY OF QUEENSLAND COLLECTION

MATTHEW C. NG

Ng, M.C. 2002 5 31: Catalogue of meteorites, tektites and associated material from the University of Queensland collection. *Memoirs of the Queensland Museum* 48(1): 173-180. Brisbane. ISSN 0077-8835.

Meteorites, tektites and associated material held in the University of Queensland earth sciences collection is listed. The catalogue of meteorites in the Queensland Museum collection is also updated with recent additions to the collection. Specimen numbers, locality, weight and, where possible, references are given for each meteorite specimen. □ *Catalogue, meteorite, tektite, University of Queensland, Queensland Museum.*

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In 1999 the earth sciences collection held by the University of Queensland (UQ) was transferred to the Queensland Museum (QMD). Meteorites, tektites and associated material in the UQ collection are listed herein along with additions to the catalogue of meteorite in the Queensland Museum (Volk, 1994).

Listed classification of meteorites follows Buchwald (1975) and Rubin (1997).

METEORITES

Gladstone number 2 Meteorite

QMD14014, shavings, bulk; 168.3g.

TYPE. Og, group IAB.

LOCALITY. Dalgety Downs, WA

REFERENCE. Richards (1930) & Buchwald (1975: 593).

Maroo Meteorite

QMD17965, tiny fragment from a mass of 236g: 0.3g.

TYPE. LL6.

LOCALITY. Found in 1991, at 25°44'S; 142°57'E central western Qld.

REFERENCE. Wlotzka (1994).

REMARKS. Donated by Western Australian Museum.

Whitula Creek Meteorite

QMD17966, 17967, fragments from a mass of 271g: 2.8g and 3.8g, respectively.

TYPE. H5.

LOCALITY. Ingella Station (25°18.95'S 142°26.68'E), Qld, coll 1992.

REFERENCE. Wlotzka (1994).

REMARKS. Donated by Western Australian Museum.

Tookabarnoo Meteorite

QMD17968, tiny fragment from a mass of 157g: 6.2g.

TYPE. H4.

LOCALITY. Found in 1992, near Tookabarnoo Waterhole (25°52' S 141°44' E), Qld.

REFERENCE. Wlotzka (1994).

REMARKS. Donated by Western Australian Museum.

Wynella Meteorite

QMD18222, cut specimen (455.8g) collected in 1997.

TYPE. H4.

LOCALITY. Near Dirranbandi, Qld.

REFERENCE. Krinov (1968).

Imilac Meteorite

QMD18491, polished slice with yellow olivine. Donated by B. Eisler; 88.6g.

TYPE. PAL.

LOCALITY. Atacama Desert, Chile.

REFERENCE. Buchwald (1975: 1393).

Binya Meteorite

QMD18496, type specimen; 34.7g.

TYPE. Og; group IIIF.

LOCALITY. Found in 1981 at Binya, central NSW.

REFERENCE. Grossman (2000).

Canyon Diablo Meteorite

QMD18989, ex-Stan Colliver collection, 20.3g.

TYPE. Og; group I.

LOCALITY. Canyon Diablo, Coconino County (35°03'N, 111°02' W), Arizona, USA.

REFERENCE. Buchwald (1975: 381).

PSEUDOMETEORITES

Weathered meteorite?

QMD7964, 8 rough specimens, magnetic, containing nickel and copper traces. Meteoritic origin doubtful; 235g, 243.2g, 170.6g, 66.4g, 26.1g, 14.3g, 11.5g, 5.5g.

LOCALITY. Reids Creek, 12 miles W of Mt. Perry, Qld.

Meteoritic iron?

QMD17213, non-magnetic, meteoritic origin doubtful; 91.5g.

LOCALITY. Cranbourne, Victoria, NSW.

Meteorite?

QMD19354, magnetic, with a sub-metallic lustre, found in laterite; 451.7g.

LOCALITY. Gove, N.T.

TEKTITES**Australites**

QMD13762a, 5.7g, core. QMD13762b, 5.6g, worn core. QMD13762c, 3.4g, indicator.

LOCALITY. Murray River Valley.

Indochinite

QMD19354, 87.5g, dumb-bell shape.

LOCALITY. Guandong Province, South China.

REMARKS. Purchased in China.

Australites

QMD13899, 0.7g, part of flange; QMD19368, 1.4g, core; QMD19369, 0.6g, water-worn core; QMD19370, 1.6g, lens; QMD19371, 0.5g, fragment; QMD19372, 1.4g, core; QMD19373, 1.6g, fragment; QMD19374, 1.0g, lens; QMD19375, 0.8g, fragment; QMD19376, 1.8g, core; QMD19377, 1.1g, elongated core; QMD19378, 1.3g, indicator; QMD19379, 0.3g, chip; QMD19380, 0.8g, chip; QMD19381, 0.8g, chip; QMD19382, 1.3g, lens; QMD19383, 0.6g, lens; QMD19384, 1.1g, chipped lens; QMD19385, 2.2g, water-worn core; QMD19386, 0.5g, core; QMD19387, 1.5g, fragment; QMD19388, 0.5g, lens; QMD19389, 0.6g, lens; QMD19390, 2.4g, elongated fragment; QMD19391, 0.5g, chip; QMD19392, 0.5g, lens; QMD19393, 0.9g, fragment; QMD19394, 0.3g, chip; QMD19395, 2.6g, water-worn fragment; QMD19396, 0.8g, water-worn fragment; QMD19397, 0.7g, indicator; QMD19398, 2.2g, fragment; QMD19399, 0.7g, indicator; QMD19400, 1.2g, water-worn core; QMD19401, 0.3g, lens; QMD19402, 0.6g, fragment of a lens; QMD19403, 1.4g, lens; QMD19404, 1.2g, core; QMD19405, 1.5g, fragment; QMD19406, 1.1g, water-worn fragment; QMD19407, 0.8g, water-worn fragment; QMD19408, 0.8g, core; QMD19409, 0.9g, core; QMD19410, 1.8g, pseudotektite; QMD19411, 0.5g, fragment; QMD19412, 1.4g, fragment; QMD19413, 0.8g, indicator; QMD19414, 0.5g, lens; QMD19415, 1.7g, irregular fragment; QMD19416, 1.0g, irregular fragment; QMD19417, 1.4g, elongated; QMD19418, 1.0g, chipped elongate; QMD19419, 2.1g, water-worn core; QMD19420, 0.8g, part of flange; QMD19421, 1.1g, water-worn fragment; QMD19422, 0.4g, eroded core; QMD19423, 0.9g, lens; QMD19424, 0.8g, half lens; QMD19425, 0.8g, lens; QMD19426, 0.5g, core; QMD19427, 1.1g, indicator; QMD19428, 0.5g, part of flange; QMD19429, 1.6g, water-worn fragment; QMD19430, 0.7g, chip; QMD19431, 1.7g, flange; QMD19432, 0.8g, lens; QMD19433, 1.7g, chip; QMD19434, 0.5g, core;

QMD19435, 1.0g, core; QMD19436, 2.5g, indicator; QMD19437, 1.0g, fragment; QMD19438, 2.0g, core; QMD19439, 0.3g, chip; QMD19440, 1.7g, water-worn fragment; QMD19441, 1.0g, water-worn fragment; QMD19442, 3.4g, water-worn indicator; QMD19443, 2.1g, water-worn fragment; QMD19444, 0.7g, lens; QMD19445, 0.6g, chip; QMD19446, 1.1g, fragment; QMD19447, 0.4g, part of flange; QMD19448, 0.6g, part of lens; QMD19449, 0.5g, chip; QMD19450, 0.9g, lens; QMD19451, 0.7g, part of button; QMD19452, 0.4g, chip; QMD19453, 0.4g, lens; QMD19454, 0.5g, fragment; QMD19455, 1.6g, fragment; QMD19456, 1.1g, eroded core; QMD19457, 0.7g, part of flange; QMD19458, 1.0g, elongated fragment; QMD19459, 2.8g, core; QMD19460, 1.6g, irregular; QMD19461, 1.4g, part of button; QMD19462, 1.0g, elongated lens; QMD19463, 2.4g, water-worn fragment; QMD19464, 1.5g, chip; QMD19465, 1.3g, water-worn fragment; QMD19466, 1.0g, chip; QMD19467, 1.2g, water-worn fragment; QMD19468, 1.2g, elongated core; QMD19469, 1.0g, lens; QMD19470, 0.8g, lens; QMD19471, 0.6g, lens; QMD19472, 0.8g, chip; QMD19473, 0.7g, chip; QMD19474, 0.6g, chip; QMD19475, 1.0g, lens; QMD19476, 0.6g, lens; QMD19477, 1.3g, water-worn fragment; QMD19478, 2.3g, water-worn fragment; QMD19479, 0.6g, lens; QMD19480, 2.0g, indicator; QMD19481, 1.1g, lens; QMD19482, 0.7g, lens; QMD19483, 1.2g, chip; QMD19484, 1.7g, fragment; QMD19485, 0.6g, chip; QMD19486, 1.2g, lens; QMD19487, 1.5g, part of button; QMD19488, 0.9g, lens; QMD19489, 0.6g, lens; QMD19490, 1.7g, lens; QMD19491, 2.4g, fragment; QMD19492, 1.4g, lens; QMD19493, 0.9g, fragment; QMD19494, 0.9g, chip; QMD19495, 2.6g, fragment; QMD19496, 1.5g, lens; QMD19497, 0.9g, fragment; QMD19498, 0.6g, lens; QMD19499, 0.5g, fragment of lens; QMD19500, 1.9g, water-worn fragment; QMD19501, 2.8g, elongated; QMD19502, 0.5g, lens; QMD19503, 2.1g, irregular; QMD19504, 1.8g, irregular; QMD19505, 0.5g, irregular; QMD19506, 2.0g, water-worn; QMD19507, 1.2g, water-worn button; QMD19508, 1.6g, water-worn; QMD19509, 0.7g, water-worn; QMD19510, 1.5g, fragment; QMD19511, 0.7g, lens; QMD19512, 0.6g, water-worn; QMD19513, 0.6g, chip; QMD19514, 0.5g, chip; QMD19515, 0.6g, lens; QMD19516, 0.9g, water-worn core; QMD19517, 0.4g, water-worn indicator; QMD19518, 1.5g, water-worn fragment; QMD19519, 0.6g, lens; QMD19520, 1.2g, lens fragment; QMD19521, 0.9g, lens fragment; QMD19522, 0.8g, fragment; QMD19523, 0.4g, chip; QMD19524, 0.5g, pseudotektite?; QMD19525, 0.4g, lens; QMD19526, 0.8g, part of flange; QMD19527, 0.4g, water-worn; QMD19528, 0.8g, lens; QMD19529, 1.4g, elongate fragment; QMD19530, 0.8g, fragment; QMD19531, 0.2g, elongated disc; QMD19532, 0.4g, chip; QMD19533, 0.4g, pseudotektite; QMD19534, 1.9g, water-worn; QMD19535, 0.6g, lens; QMD19536, 0.3g, chip; QMD19537, 0.6g, fragment; QMD19538, 1.1g, chipped fragment; QMD19539, 1.4g, lens; QMD19540, 0.8g, fragment

LOCALITY. South Australia.

UNIVERSITY OF QUEENSLAND EARTH
SCIENCES COLLECTION

METEORITES

Canyon Diablo Meteorite

UQ11151, UQ11152, missing.

LOCALITY. Barringer Meteor Crater, Northern Arizona, USA.

REMARKS. Purchased Scott Williams.

Gilgoi Meteorite

UQ11159, missing.

TYPE. H5.

LOCALITY. Gilgoi, New South Wales.

REFERENCE. Prior (1923; p. 64).

McKinney Meteorite

UQ11160, 2 specimens and 2 thin sections; 56.3g, 4.8g.

TYPE. Possibly hypersthene-chondrite (L4?).

LOCALITY. McKinney, Texas (USA).

REFERENCE. Prior (1923; p. 110).

Henbury Meteorite

UQ30122: 4.6kg; UQ31027: 137.3g; UQ30128: 132.2g; UQ30130: 52.4g; UQ30131: 45.5g; UQ30132: 27.2g; UQ30133: 28g; UQ30134: 36.5g; UQ30135: 37g; UQ30136: 20.9g; UQ30137: 4.7g; UQ30138: 16.7g; UQ30139: 18.3g. Missing: UQ11161, UQ11163, UQ30121, UQ30123-30126, UQ30129, UQ30140-UQ30144.

TYPE. Om; group IIIA.

LOCALITY. Henbury, S.A.

REFERENCE. Buchwald (1975; p. 638).

Molong PMG

UQ11162, 2 weathered rough specimens; 225g, 167.8g.

TYPE. Class PAL (normal PMG).

LOCALITY. Molong, NSW.

REFERENCE. Prior (1923; p. 116).

Glenormiston Meteorite

UQ11193, brecciated rough specimen: 536.1g.

TYPE. Om.

LOCALITY. 10km south of Glenormiston, western Qld.

REFERENCE. Richards (1930) & Buchwald (1975; p. 596).

Canyon Diablo Meteorite

UQ12416, fragment; 90.3g.

LOCALITY. Barringer Crater, near Winslow, Arizona, USA.

Tenham Meteorite

UQ12612, 908g; UQ12613, 340g. Missing

TYPE. H5.

LOCALITY. 'Ingella' Station, 25°33'S 142°48'E (Tenham Station, Kyabra Creek. 50km south east of Windorah, Queensland).

REMARKS. Collector Mr. Hammond, 1939.

Box Hole Meteorite

UQ29272, missing

TYPE. Om; group IIIA.

LOCALITY. Box Hole, NT.

Wolf Creek Meteorite

UQ29273, 6 tiny fragments; 1.9g, 4.2g, 8.0g, 3.5g, 2.2g, 2.7g.

TYPE. Om; group IIB.

LOCALITY. Wolf Creek Crater, WA.

REFERENCE. Buchwald (1975; p. 1327).

Wolf Creek Meteorite

UQ30145, rough specimen; 14.9g.

TYPE. Om; group IIB.

LOCALITY. Wolf Creek 640km east of Broome, WA.

REFERENCE. As for UQ29273.

Boxhole Meteorite

UQ30146, 1 rough specimen; 18.3g.

TYPE. Om; group IIIA.

LOCALITY. Box Hole 19.2km N.E. of Alice Springs, Northern Territory.

REFERENCE. Buchwald (1975; p. 338).

Boxhole Meteorite?

UQ30147-UQ30151, purchased from aborigines; 15.0g, 9.2g, 7.6g, 4.5g, 7.0g.

TYPE. Om; group IIIA.

LOCALITY. St. Vigeins Cattle Station, Northern Territory.

Iron meteorite

UQ34849, 15.6kg.

TYPE. Iron.

LOCALITY. unknown.

Tuxtuac Meteorite

UQ43005, from the main mass. Fell 16th Oct. 1975; 1g. Missing

TYPE. 'Amphoterite' Olivine-hypersthene chondrite (LL5)

LOCALITY. Tuxtuac, Mexico.

REMARK: Exchanged by Rainer Bartoschewitz, west Germany.

REFERENCE. Graham (1981).

Toluca Meteorite

UQ43007, thick slice; 62.7g.

TYPE. Og, group I.

LOCALITY. Found in 1776 Toluca, Mexico.

REFERENCE. Buchwald (1975; p. 1209).

Allende Meteorite

UQ43008, fell 8th Feb. 1969; weight 40.4g. Missing TYPE. Carbonaceous chondrite (CV3).

LOCALITY. Allende, Mexico.

REMARK: Exchanged by Rainer Bartoschewitz, west Germany.

REFERENCE. Clarke et al. (1971) & Buchwald (1975).

PSEUDOMETEORITE**Aerolites?**

UQM565, 3 samples. Meteoritic origin questionable; 265.5g, 127.1g, 109.2g.

LOCALITY. Quetta.

TEKTITES**Australites**

UQ5852/1, 0.9g, lens; UQ5852/2, 0.8g, chipped lens; UQ5852/3, 0.6g, chipped fragment; UQ5852/4, 1.6g, water-worn; UQ5852/5, 1.6g, lens; UQ5852/6, 2.3g, lens; UQ5852/7, 9.1g, core; UQ5852/8, 2.8g, elongate; UQ5852/9, 1.8g, elongate; UQ5852/10, 3.5g, apioid; UQ30065, 0.4g, lens; UQ30066, 0.7g, core; UQ30067, 2.2g, lens; UQ30068, 3.6g, core; UQ30069, 7.3g, core; UQ30070, 1g, apioid?; UQ30071, 1.6g, ellipsoid core; UQ30072, 0.8g, apioid core; UQ30073, 2.5g, core; UQ30074, 1.2g, fragment; UQ30075, 0.6g, lens; UQ30076, 1.4g, lens; UQ30077, 6.3g, chipped lens; UQ30078, 1.4g, water-worn core; UQ30079, 2.7g, fragment; UQ30080, 1.0g, elongate fragment; UQ30081, 2.0g, apioid.

LOCALITY. Mooraberrie, Qld.

Indochinite

UQ11157, 1.5g, irregular.

LOCALITY. Thailand.

Australite

UQ11192, a thin section of an australite(?).

LOCALITY. Unknown.

Indochinite

UQ16373, 5.2g, irregular.

LOCALITY. Indo-china.

Australites

UQ29500, 2.8g, indicator; UQ29501, 3.0g, indicator; UQ29502, 3.3g, indicator; UQ29503, 3.2g, indicator; UQ29504, 2.7g, indicator; UQ29505, 2.0g, indicator; UQ29506, 2.2g, indicator; UQ29507, 1.6g, indicator; UQ29508, 1.8g, indicator; UQ29509, 1.1g, indicator; UQ29510, 2.1g, indicator; UQ29511, 1.5g, indicator; UQ29512, 3.8g, indicator; UQ29513, 3.2g, indicator; UQ29514, 2.7g, indicator; UQ29515, 2.0g, indicator; UQ29516, 3.1g, indicator; UQ29517, 2.1g, indicator; UQ29518, 2.9g, indicator; UQ29519, 1.9g, indicator; UQ29520, 3.1g, indicator; UQ29521, 2.3g, indicator; UQ29522, 1.3g, indicator; UQ29523, 2.9g, indicator; UQ29524, 1.3g, indicator; UQ29525, 2.0g, indicator;

UQ29526, 2.5g, indicator; UQ29527, 2.8g, indicator; UQ29528, 0.9g, indicator; UQ29529, 1.2g, indicator; UQ29530, 4.2g, indicator; UQ29531, 1.2g, indicator; UQ29532, 0.6g, indicator; UQ29533, 0.9g, indicator; UQ29534, 1.4g, indicator; UQ29535, 2.0g, indicator; UQ29536, 1.0g, indicator; UQ29537, 1.6g, indicator; UQ29538, 1.1g, indicator; UQ29539, 1.7g, indicator; UQ29540?, 1.9g, indicator; UQ29541, 1.8g, indicator; UQ29542, 3.1g, core; UQ29543, 1.5g, indicator; UQ29544, 2.0g, indicator; UQ29545, 2.0g, indicator; UQ29546, 2.8g, chipped indicator; UQ29547, 6.3g, chipped core; UQ29548, 2.3g, chipped indicator; UQ29549, 2.1g, chipped indicator; UQ29550, 1.6g, lens?; UQ29551, 2.7g, lens?; UQ29552, 1.7g, flange fragment; UQ29553, 1.6g, core?; UQ29554, 2.7g, core?; UQ29555, 2.5g, core?; UQ29556, 0.8g, flange; UQ29557, 2.6g, indicator; UQ29558, 1.5g, lens?; UQ29559, 1.0g, lens?; UQ29560, 2.1g, eroded core?; UQ29561, 1.5g, lens?; UQ29562, 1.6g, indicator; UQ29563, 2.5g, eroded core?; UQ29564, 2.3g, eroded button; UQ29565, 2.0g, indicator; UQ29566, 1.2g, chipped lens; UQ29567, 2.4g, fragment; UQ29568, 2.2g, eroded indicator; UQ29569, 3.2g, fragment; UQ29570, 2.8g, chipped eroded core; UQ29571, 3.3g, eroded core; UQ29572, 1.9g, fragment; UQ29573, 1.7g, indicator; UQ29574, 2.5g, eroded indicator; UQ29575, 1.5g, eroded lens; UQ29576, 1.9g, eroded core?; UQ29577, 1.5g, chipped lens; UQ29578, 2.1g, chipped lens; UQ29579, 1.9g, eroded indicator; UQ29580, 1.6g, indicator; UQ29581, 1.9g, eroded lens; UQ29582, 1.8g, eroded indicator; UQ29583, 1.4g, eroded indicator; UQ29584, 1.4g, indicator; UQ29585, 1.6g, chipped eroded lens; UQ29586, 1.6g, eroded core; UQ29587, 2.1g, chipped indicator; UQ29588, 1.2g, lens; UQ29589, 3.1g, indicator; UQ29590, 2.3g, indicator; UQ29591, 1.1g, eroded lens; UQ29592, 1.7g, chipped lens; UQ29593, 1.0g, fragment of lens; UQ29594, 1.8g, eroded lens; UQ29595, 1.2g, eroded core?; UQ29596, 1.1g, Chip; UQ29597, 1.0g, Chip; UQ29598, 1.3g, eroded indicator; UQ29599, 1.7g, eroded indicator; UQ29600, 2.1g, eroded lens; UQ29601, 1.7g, indicator; UQ29602, 0.8g, lens; UQ29603, 0.8g, lens; UQ29604, 1.9g, eroded indicator; UQ29605, 1.2g, fragment; UQ29606, 1.6g, eroded fragment; UQ29607, 1.6g, eroded indicator; UQ29608, 2.5g, indicator?; UQ29609, 1.3g, eroded lens; UQ29610, 1.4g, chipped fragment; UQ29611, 1.6g, chipped indicator; UQ29612, 1.2g, chipped indicator; UQ29613, 2.2g, chipped indicator; UQ29614, 1.9g, indicator; UQ29615, 1.4g, fragment; UQ29616, 1.3g, indicator; UQ29617, 0.8g, fragment; UQ29618, 1.1g, lens; UQ29619, 1.1g, indicator; UQ29620, 2.0g, lens; UQ29621, 0.4g, fragment; UQ29622, 1.1g, chipped lens; UQ29623, 2.3g, indicator; UQ29624, 1.8g, fragment; UQ29625, 2.5g, eroded fragment; UQ29626, 1.2g, eroded core; UQ29627, 1.2g, eroded core?; UQ29628, 1.4g, indicator; UQ29629, 1.9g, fragment; UQ29630, 4.2g, eroded fragment; UQ29631, 2.3g, fragment of a core?; UQ29632, 1.0g, chipped lens; UQ29633, 2.4g, fragment; UQ29634, 1.7g, chip from a elongate core; UQ29635, 2.4g, eroded lens; UQ29636, 1.2g, fragment; UQ29637, 1.7g, fragment; UQ29638, 1.6g, fragment; UQ29639, 1.1g, fragment; UQ29640, 2.4g, fragment; UQ29641,

4.8g, eroded elongated core; UQ29642, 8.4g, fragment; UQ29643, 13.3g, fragment; UQ29644, 9.8g, fragment; UQ29645, 3.2g, fragment; UQ29646, 5.7g, fragment; UQ29647, 2.9g, chip fragment; UQ29648, 0.8g, chip from button (flange?); UQ29649, 4.1g, chip fragment; UQ29650, 2.6g, lens; UQ29651, 1.9g, core; UQ29652, 3.2g, Irregular core; UQ29653, 2.8g, fragment; UQ29654, 2.0g, eroded indicator; UQ29655, 1.9g, broken lens; UQ29656, 1.9g, fragment; UQ29657, 0.8g, fragment; UQ29658, 2.0g, fragment; UQ29659, 3.0g, Irregular shape; UQ29660, 1.8g, indicator; UQ29661, 2.1g, fragment; UQ29662, 2.4g, smoothed fragment; UQ29663, 2.3g, eroded lens; UQ29664, 2.9g, lens?; UQ29665, 2.0g, fragment of core?; UQ29666, 2.9g, fragment; UQ29667, 2.2g, chip of a indicator; UQ29668, 1.7g, fragment; UQ29669, 2.0g, chip fragment; UQ29670, 2.6g, fragment; UQ29671, 2.0g, fragment; UQ29672, 1.3g, fragment; UQ29673, 0.9g, fragment; UQ29674, 0.6g, elongated; UQ29675, 0.9g, elongated; UQ29676, 1.9g, elongated; UQ29677, 1.9g, elongated; UQ29678, 1.8g, elongated; UQ29679, 1.4g, elongated; UQ29680, 14.3g, elongated; UQ29681, 5.9g, elongated; UQ29682, 5.6g, elongated; UQ29683, 4.2g, elongated; UQ29684, 5.9g, elongated; UQ29685, 7.8g, elongated; UQ29686, 4.8g, elongated; UQ29687, 2.3g, elongated; UQ29688, 6.5g, elongated; UQ29689, 4.0g, elongated; UQ29690, 3.0g, elongated; UQ29691, 3.7g, elongated; UQ29692, 3.4g, elongated; UQ29693, 3.1g, elongated; UQ29694, 3.8g, elongated; UQ29695, 2.7g, elongated; UQ29696, 2.0g, elongated; UQ29697, 2.9g, elongated; UQ29698, 3.8g, elongated; UQ29699, 2.6g, elongated; UQ29700, 3.9g, elongated; UQ29701, 1.6g, elongated; UQ29702, 2.6g, elongated; UQ29703, 1.1g, elongated; UQ29704, 4.0g, elongated; UQ29705, 2.2g, elongated; UQ29706, 4.1g, elongated; UQ29707, 3.3g, indicator; UQ29708, 4.4g, fragment; UQ29709, 2.4g, fragment; UQ29710, 10.0g, fragment; UQ29711, 2.0g, fragment; UQ29712, 2.2g, fragment; UQ29713, 3.1g, fragment; UQ29714, 2.2g, fragment; UQ29715, 1.8g, fragment; UQ29716, 0.9g, fragment; UQ29717, 1.9g, fragment; UQ29718, 1.3g, fragment; UQ29719, 1.8g, fragment; UQ29720, 1.8g, fragment; UQ29721, 1.6g, fragment; UQ29722, 1.1g, fragment; UQ29723, 1.8g, fragment; UQ29724, 0.8g, fragment; UQ29725, 1.0g, fragment; UQ29726, 0.8g, fragment; UQ29727, 1.3g, fragment; UQ29728, 1.5g, fragment; UQ29729, 1.1g, fragment; UQ29730, 0.6g, fragment; UQ29731, 1.1g, fragment; UQ29732, 1.1g, fragment; UQ29733, 1.1g, fragment; UQ29734, 5.1g, fragment; UQ29735, 2.0g, fragment; UQ29736, 2.4g, fragment; UQ29737, 2.2g, fragment; UQ29738, 2.1g, fragment; UQ29739, 1.5g, fragment; UQ29740, 1.4g, Part of flange; UQ29741, 1.8g, fragment; UQ29742, 1.8g, fragment; UQ29743, 1.4g, fragment; UQ29744, 1.3g, fragment; UQ29745, 0.7g, fragment; UQ29746, 1.6g, fragment; UQ29747, 0.7g, fragment; UQ29748, 0.9g, fragment; UQ29749, 0.8g, fragment; UQ29750, 0.8g, fragment; UQ29751, 0.5g, fragment; UQ29752, 0.4g, fragment; UQ29753, 0.9g, fragment; UQ29754, 12.9g, hollows (skin off buttons); UQ29755, 11.6g, hollows (skin off buttons); UQ29756, 3.3g, hollows (skin off buttons); UQ29757, 1.9g, hollows (skin off buttons); UQ29758, 2.4g, chips;

UQ29759, 1.4g, chips; UQ29760, 1.1g, chips; UQ29761, 2.0g, chips; UQ29762, 2.4g, chips; UQ29763, 9.1g, chips; UQ29764, 3.5g, chips; UQ29765, 1.9g, chips; UQ29766, 3.3g, chips; UQ29767, 2.9g, chips; UQ29768, 3.2g, chips; UQ29769, 3.4g, chips; UQ29770, 4.4g, chips; UQ29771, 5.0g, chips; UQ29772, 3.1g, chips; UQ29773, 0.4g, chips; UQ29774, -, Missing; UQ29775, 1.1g, chips; UQ29776, 1.8g, chips; UQ29777, 2.4g, chips; UQ29778, 3.1g, chips; UQ29779, 3.4g, chips; UQ29780, 1.9g, chips; UQ29781, 3.6g, chips; UQ29782, 2.0g, chips; UQ29783, 0.5g, chips; UQ29784, 0.8g, chips; UQ29785, 0.7g, chips; UQ29786, 1.1g, chips; UQ29787, 1.1g, chips; UQ29788, 0.4g, chips.

LOCALITY. North corner Lake Cuddapan, Queensland. East of Betoota (141°26'E 25°43'S). Coll. G. Hume, 1971. NOTE. 'L. Cuppapa'.

Philippinites

UQ29789, 35.9g, sphere; UQ29790, 32.5g, sphere; UQ29791, 29.4g, sphere; UQ29792, 30.5g, sphere; UQ29793, 27.9g, sphere; UQ29794, 21.8g, sphere; UQ29795, 19.1g, sphere; UQ29796, 18.8g, sphere; UQ29797, 18.9g, sphere; UQ29798, 11.7g, sphere; UQ29799, 12.9g, sphere; UQ29800, 14.5g, sphere; UQ29801, 11.7g, sphere; UQ29802, 9.7g, sphere; UQ29803, 6.8g, sphere; UQ29804, 9.9g, sphere; UQ29805, 9.5g, sphere; UQ29806, 11.6g, sphere; UQ29807, 10.1g, sphere; UQ29808, 7.2g, sphere; UQ29809, 8.7g, sphere; UQ29810, 5.9g, flattened ovate; UQ29811, 9.6g, flattened ovate; UQ29812, 4.9g, flattened ovate; UQ29813, 7.0g, sphere; UQ29814, 11.2g, sphere; UQ29815, 5.9g, irregular; UQ29816, 7.7g, irregular; UQ29817, 7.6g, irregular; UQ29818, 5.1g, sphere; UQ29819, 3.9g, sphere; UQ29820, 2.8g, sphere; UQ29821, 4.2g, sphere; UQ29822, 2.3g, sphere; UQ29823, 4.7g, chip; UQ29824, 1.9g, irregular; UQ29825, -, missing; UQ29826, 19.4g, elongate; UQ29827, 13.1g, elongate; UQ29828, 7.6g, elongate; UQ29829, 12.5g, apioid; UQ29830, 6.0g, apioid; UQ29890, -, missing

LOCALITY. Pugad-babuy Site, Bulakan Province, Luzon Island, Philippines. Coll. Otley Beyar & F.W. Whitehouse.

UQ29831, -, missing (billitonite); UQ29832, -, missing (billitonite); UQ29833, 17.7g, billitonite; UQ29834, 17.8g, billitonite; UQ29835, 18.5g, billitonite; UQ29836, 6.1g, billitonite; UQ29837, 5.2g, billitonite; UQ29838, 13.1g, billitonite; UQ29839, 9.5g, billitonite; UQ29840, 8.0g, billitonite; UQ29841, 14.7g, billitonite.

LOCALITY. Maysan Site, Bulakan Province, Luzon Island, Philippines. Coll. Otley Beyar & F.W. Whitehouse.

UQ29842, 28.5g, sphere; UQ29843, 28.0g, sphere; UQ29844, 15.0g, sphere; UQ29845, 16.0g, sphere; UQ29846, 14.7g, sphere; UQ29847, 4.5g, sphere; UQ29848, 7.8g, sphere; UQ29849, 5.3g, sphere; UQ29850, 4.8g, sphere; UQ29851, 4.1g, sphere; UQ29852, 33.2g, flattened sphere; UQ29853, 3.8g, flattened sphere; UQ29854, 27.8g, elongate; UQ29855, 33.0g, elongate; UQ29856, 19.4g, elongate; UQ29857, 16.0g, elongate; UQ29858, 16.5g, elongate; UQ29859,

8.6g, elongate; UQ29860, 10.5g, apicoid; UQ29861, 6.5g, apicoid; UQ29862, 4.0g, irregular; UQ29863, 1.6g, irregular; UQ29864, 1.7g, irregular; UQ29865, 2.5g, irregular; UQ29866, 2.2g, irregular; UQ29867, 1.1g, irregular; UQ29868, 1.4g, irregular; UQ29869, 0.9g, irregular; UQ29870, 1.2g, irregular; UQ29871, 2.1g, irregular; UQ29872, 0.7g, irregular; UQ29873, 1.0g, irregular; UQ29874, 0.6g, irregular; UQ29875, 2.6g, sphere; UQ29876, 0.8g, irregular; UQ29877, 1.0g, irregular; UQ29878, 0.7g, irregular; UQ29879, 1.5g, flattened sphere; UQ29880, 2.3g, sphere; UQ29881, 1.9g, sphere; UQ29882, 0.6g, 'Moldavite-like'; UQ29883, 1.2g, 'Moldavite-like'; UQ29884, 5.8g, pseudo-australite.

LOCALITY. Santo Mesa Rizal Province, Luzon Island, Philippines. Coll. Otley Beyar & F.W. Whitehouse.

UQ29885, 20.0g, irregular; UQ29886, 12.9g, irregular; UQ29887, 5.7g, irregular; UQ29888, 7.9g, irregular (slightly discoloured by fire); UQ29889, 9.2g, irregular (slightly discoloured by fire).

LOCALITY. Kubao Site, Ribal Province, Luzon Island, Philippines. Coll. Otley Beyar & F.W. Whitehouse.

UQ29891, 84.6g, irregular; from inland placer near Balhaloni; UQ29892, 132.1g, Spherical; specimen buried Coco Grove placers at Paraolol.

LOCALITY. Bikol Site, Catambines Norte Province, Luzon, Philippines. Coll. Otley Beyar & F.W. Whitehouse.

UQ29893, 15.6g, irregular; UQ29894, 8.6g, irregular; UQ29895, 4.6g, irregular; UQ29896, 2.7g, irregular; UQ29897, 2.3g, irregular.

LOCALITY. Busuanga Island, Philippines. (Kalamian or Busuanga Tektites). Coll. Otley Beyar & F.W. Whitehouse.

Phil-amerikanites

UQ29898, -, missing; UQ29899, 8.5g, irregular; UQ29900, 6.9g, irregular; UQ29901, 6.4g, irregular; UQ29902, 3.3g, irregular; UQ29903, 4.4g, irregular; UQ29904, 5.8g, irregular; UQ29905, 2.5g, irregular; UQ29906, 3.1g, irregular; UQ29907, 2.5g, irregular; UQ29908, 0.6g, irregular; UQ29909, 3.0g, chip; UQ29910, 0.3g, irregular; UQ29911, 21.3g, sub-spherical; UQ29912, 13.4g, Sub-spherical; UQ29913, 13.9g, sub-spherical; UQ29914, 3.5g, sub-spherical; UQ29915, 17.2g, elongated; UQ29916, 3.3g, sub-oval; UQ29917, 12.2g, elongated; UQ29918, 9.5g, elongated; UQ29919, 11.0g, irregular; UQ29920, 3.1g, sub-spherical; UQ29921, 0.5g, irregular.

LOCALITY. Santa-Mesa Site, Rizal Province, suburb of Manila. Coll. Otley Beyar & F.W. Whitehouse.

Australites

UQ29923, 3.0g, half indicator; UQ29924, 3.8g, indicator; UQ29925, 3.5g, indicator; UQ29926, 2.7g, indicator; UQ29927, 1.7g, lens; UQ29928, -, missing; UQ29929, 5.8g, core; UQ29930, 5.0g, core; UQ29931, 3.3g, lens; UQ29932, 8.2g, sub-spherical; UQ29933, 13.7g, core; UQ29934, 6.5g, core; UQ29935, -, missing; UQ29936, -,

missing; UQ29937, 4.3g, core; UQ29938, 4.8g, core; UQ29939, 3.1g, core; UQ29940, -, missing; UQ29941, 6.0g, elongate; UQ29942, -, missing; UQ29943, 5.5g, elongate; UQ29944, 5.9g, elongate; UQ29945, 3.4g, elongate; UQ29946, -, missing; UQ29947, 4.9g, elongate; UQ29948, 19.1g, core; UQ29949, 15.9g, core?; UQ29950, 9.0g, fragment; UQ29951, 8.1g, fragment; UQ29952, -, missing; UQ29953, 17.8g, apicoid; UQ29954, 3.2g, water-worn fragment; UQ29955, 2.5g, water-worn fragment; UQ29956, 1.8g, conical; UQ29957, 1.7g, conical; UQ29958, 1.6g, boat-shaped lens; UQ29959, 12.5g, elongate (dumbbell); UQ30061, 9.9g, circular core; UQ30062, 6.2g, core; UQ30063, 6.2g, lens; UQ30082, 3.5g, water-worn and clipped core.

LOCALITY. Charlotte Waters, NT. Coll. F.W. Whitehouse (30061-30063). Coll. Otley Beyar & F.W. Whitehouse.

UQ29960, 18.5g, spherical; UQ29961, 6.9g, core; UQ29962, 4.8g, core; UQ29963, 4.6g, non-descriptive; UQ29964, 7.1g, elongate; UQ29965, 14.8g, elongate.

LOCALITY. Todmorden, South Australia.

UQ29966, -, missing; UQ29967, 2.2g, indicator; UQ29968, 21.3g, core; UQ29969, 8.5g, core; UQ29970, 16.4g, half of a core; UQ29971, 12.0g, core; UQ29972, 7.2g, core; UQ29973, 4.8g, elongate (dumbbell); UQ29974, 3.6g, circular dish.

LOCALITY. Bloods Creek, South Australia.

UQ29975, 31.5g, core?; UQ30083, 30.1g, water-worn core.

LOCALITY. 160km east of Alice Springs (?), Central Australia. Coll. Mr McDill.

UQ29976, 10.5g, water-worn core?; UQ29977, 13.0g, spherical; UQ29978, 4.7g, elongate core?; UQ30084, 11.6g, water-worn core; UQ30085, 1.3g, Half dumbbell; UQ30086, 31.8g, fractured spheroid; UQ30087, 4.8g, button with part of flange missing; UQ30088, 4.2g, apicoid with flange; UQ30089, 1.0g, fragment of lens; UQ30090, 1.5g, core; UQ30091, 1.6g, core; UQ30092, 1.3g, core.

LOCALITY. Eastern Goldfields, Kalgoorlie area, WA. Coll. Otley Beyar & F.W. Whitehouse.

REMARKS. Locality for UQ30085 is marked in the register as 'Query (?)', but is given as 'Eastern Goldfields, Kalgoorlie area, WA' in curation notes.

UQ29979, 16.8g, oval core; UQ29980, 1.0g, lens.

LOCALITY. Tin fields, north Queensland.

UQ29981, 13.6g, core; UQ29982, 12.3g, core; UQ29983, 8.2g, elongate; UQ29984, 10.1g, elongate; UQ29985, 10.4g, core?; UQ29986, 5.1g, core fragment.

LOCALITY. Memory Bore, Dalhousie, South Australia.

UQ29987, 4.1g, lens; UQ29988, 0.9g, lens; UQ29989, 0.9g, lens; UQ29990, 0.7g, lens; UQ29991, 1.1g, lens; UQ29992, 10.0g, core; UQ29993, 9.7g, core; UQ29994, 6.1g, core; UQ29995, 6.0g, core; UQ29996, 5.9g, core; UQ29997, 3.3g, core; UQ29998, 2.5g, core; UQ29999, 5.0g, core; UQ30000, 7.1g, core; UQ30001, 7.8g, core; UQ30002, 2.3g, core; UQ30003, 3.4g, core; UQ30004, 14.1g, lens; UQ30005, 3.5g, lens; UQ30006, 2.2g, lens; UQ30007, 2.1g, lens; UQ30008, 1.9g, lens; UQ30009, 10.0g, ovate; UQ30010, 7.6g, ovate; UQ30011, 5.7g, ovate; UQ30012, 4.6g, ovate; UQ30013, 5.6g, ovate; UQ30014, 4.3g, ovate; UQ30015, 2.9g, ovate; UQ30016, 2.8g, ovate; UQ30017, 1.3g, ovate; UQ30018, 0.8g, ovate; UQ30019, 7.6g, ovate; UQ30020, 9.2g, ovate; UQ30021, 3.3g, ovate; UQ30022, 4.2g, ovate; UQ30023, 6.8g, ovate; UQ30024, 4.7g, ovate; UQ30025, 12.2g, core; UQ30026, 6.8g, fragment; UQ30027, 1.7g, button fragment with flange; UQ30028, 3.5g, chips; UQ30029, 1.5g, chips; UQ30030, 22.5g, chipped and weathered core; UQ30031, 18.6g, chipped specimen; UQ30032, 11.9g, water-worn core; UQ30033, 7.4g, water-worn core; UQ30034, 8.5g, water-worn core; UQ30035, 6.3g, water-worn core; UQ30036, 6.7g, water-rounded specimen; UQ30037, 4.3g, water-rounded specimen; UQ30038, 4.3g, core?; UQ30039, 10.1g, fragment; UQ30040, 4.1g, ovate core; UQ30041, 2.4g, ovate indicator; UQ30042, 1.9g, indicator; UQ30043, 0.8g, lens; UQ30044, 3.1g, water-rounded specimen?; UQ30045, 1.4g, core?; UQ30046, 1.4g, core; UQ30047, 3.8g, lens; UQ30048, 2.4g, fragment; UQ30049, 4.0g, fragment; UQ30050, 3.9g, fragment; UQ30051, 2.0g, fragment; UQ30052, 3.3g, fragment; UQ30053, 2.8g, fragment; UQ30054, 2.2g, fragment; UQ30055, 2.9g, fragment; UQ30056, 6.1g, fragment; UQ30057, 2.4g, fragment; UQ30058, 3.2g, fragment; UQ30059, 0.7g, fragment; UQ30060, 0.9g, fragment.

LOCALITY. Finnis Springs, South Australia.

UQ30064, 4.7g, water-rounded specimens.

LOCALITY. Queensland.

Moldavites

UQ30093, 3.5g; UQ30094, 2.0g; UQ30095, 3.6g; UQ30096, 2.7g; UQ30097, 4.2g; UQ30098, 1.8g; UQ30099, 10.0g; UQ30100, 3.8g; UQ30101, 6.1g; UQ30102, 5.1g; UQ30103, -, missing; UQ30104, 2.5g; UQ30105, -, missing; UQ30106, 2.3g; UQ30107, 2.7g; UQ30108, 1.5g; UQ30112, 1.9g; UQ30113, 1.5g; UQ30114, 1.1g; UQ30115, 1.1g; UQ30116, 1.6g; UQ30117, 0.9g; UQ30118, 1.2g; UQ30119, 1.0g; UQ30120, 8.7g, bulk collection.

LOCALITY. Habn, Sundbohlen.

'Darwin glass' (impact glass)

UQ4515.

LOCALITY. 10 Mile Hill, Kelly's Basin Railway, Mt Lyell, Tasmania.

REFERENCE. Fudali & Ford (1979).

Stishovite

UQ8208

LOCALITY. Meteor Crater (Coconino County), Arizona, USA.

Stishovite and coesite

UQ11153.

LOCALITY. Northern Arizona (USA), Bominger Meteor Crater.

Lechatelierite

UQ11154

LOCALITY. Northern Arizona (USA), Bominger Meteor Crater.

Pulverised rock flour

UQ11155

LOCALITY. Northern Arizona (USA), Bominger Meteor Crater.

Aeolian sand

UQ11156

LOCALITY. Northern Arizona (USA), Bominger Meteor Crater.

Fused sand and thin section

UQ11158

LOCALITY. Impact area in Henbury, SA.

Densite rocks associated with Henbury Meteorite

UQ11161

LOCALITY. Henbury, SA.

Suevite

UQ43006

LOCALITY. Found in Quarry in Altebury, Nordinger, west Germany.

Metallic spheroids

UQM4859

LOCALITY. Arizona Meteorite Crater, Arizona (USA).

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LITERATURE CITED

- BUCHWALD, V.F. 1975. Handbook of iron meteorites: their history, distribution, composition and structure (three volumes). (University of California press: Berkeley).
- FUDALI, R.F. & FORD, R.J. 1979. Darwin glass and Darwin Crater: a progress report. *Meteoritics* 14(3): 283-296.
- GRAHAM, A.L. 1981. *Meteoritical Bulletin* 59. *Meteoritics* 16: 193-199.

- GROSSMAN, J.N. 2000. The meteoritical bulletin, 84. *Meteoritics and Planetary Science* 35: 199-225.
- KRINOV, E.L. (ed.) 1970. The meteoritical bulletin, nos 36-48. *Meteoritics* 5: 85-109.
- PRIOR, G.T. 1923. Catalogue of meteorites with specimen reference to those represented in the collection of the British Museum (Natural History). (Trustees of the British Museum (Natural History): London).
- RICHARDS, H.C. 1930. The Glenormiston Meteorite. *Memoirs of the Queensland Museum* 10: 65-72.
- RUBIN, A. 1997. Mineralogy of meteorite groups. *Meteoritics & Planetary Science* 32: 231-247.
- VOLK, P. 1994. Catalogue of meteorites, tektites and associated material in the Queensland Museum. *Memoirs of the Queensland Museum* 35(1): 255-262.
- WLOTZKA, F. (ed.) 1994. The meteoritical bulletin, 77. *Meteoritics and Planetary Science* 29: 891-897.

AUSTRALIAN RAINFOREST BIOGEOGRAPHY: IS THERE A RELICTUAL BEETLE FAUNA IN AN *ALLOSYNCARPIA* RAINFOREST REFUGIUM, ARNHEMLAND, NORTHERN TERRITORY?

STEWART B. PECK

Peck, S.B. 2002 5 31: Australian rainforest biogeography: is there a relictual beetle fauna in an *Allosyncarpia* rainforest refugium, Arnhemland, Northern Territory? *Memoirs of the Queensland Museum* 48(1): 181-192. Brisbane. ISSN 0079-8835.

It has been suggested that the *Allosyncarpia ternata* forests of western Arnhemland, Northern Territory, may be relictual and may be biotic refugia from Tertiary times. To explore the hypothesis, a study of the entire beetle fauna was made in an *A. ternata* forest in Podocarpus Canyon, a small, isolated refugial forest containing the richest recorded plant diversity in NT. At least 508 beetle species were found, belonging to 58 families and at least 318 genera. Only 47 could be named to species; new species and new records for NT were found; and most species are probably not described. Of the named species limited to rainforest, more have disjunct distributions shared with Queensland than with Western Australia. These range disjunctions can be interpreted as evidence of either long distance dispersal or fragmentation of broader former distributions. No taxa were found which seemed to be phylogenetic relicts. A total diversity of more than 2000 species of insects is calculated for the forest. It is concluded that the beetle fauna assembled itself by dispersal in Holocene times. It is not a relict (ancient) assemblage. Beetles and insects in general may be able to contribute more towards reconstructing the biogeographic history of Australia and the forest history of NT, but only when their taxonomy and distributions become better known. □ *Insecta, beetles, Allosyncarpia ternata, rainforest, refugia, Northern Territory.*

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It is generally thought that rainforest was widely (and perhaps continuously) distributed across northern Australia in the early Tertiary, and persisted until the Miocene (Truswell, 1990). Climatic change in the late Tertiary and the greatly fluctuating climates of the Pleistocene and Holocene further partitioned the rainforest of northern Australia into numerous separate and small patches as habitat islands associated with permanent moisture, scattered across a vast expanse of mostly eucalypt-dominated woodland and savanna.

The rainforest (also called monsoonal vine forest) patches of the Northern Territory are now completely isolated from both those of northern Queensland (by the Gulf of Carpentaria and the arid treeless grasslands of the Barkly Tablelands of northwestern Queensland), and from those to the west in the Kimberley Region of Western Australia (except along the coastline, and by a few riverine gallery forests). All the rainforest patches in NT and WA are concentrated in regions with higher rainfall (more than 600 mm per year), and the patches decline in size, density, species richness, and complexity westwards (Kikkawa et al., 1981; Russell-Smith, 1991).

Through support of the National Rainforest Conservation Program there is now an extensive database on rainforest vegetation in the Northern Territory and Western Australia. However, there are few studies of the insect assemblages of these forests. Compared to rainforests elsewhere in the world, Australian monsoon and wet tropical rainforests are generally thought to have an impoverished insect fauna (Anderson & Majer, 1991; Reichle & Anderson, 1996). Naumann et al. (1991) found beetles and sphecoid wasps to be less diverse in Kimberley rainforests than in adjacent savannah, and of lower diversity than in the rainforests in eastern Australia. In 8 Kimberley rainforest patches, the insects in general (Naumann et al., 1991) and ants in particular had low diversity and high species turnover between patches. Majer (1990) stated that ant faunas in northern Australian rainforests are low in diversity when compared to other tropical regions. The ant communities (Anderson & Majer, 1991) were judged to be *ad hoc* assemblages of broadly-adapted species, with only a few specialist rainforest taxa.

NT RAINFORESTS. There are two distinct types of closed canopy rainforest in the Northern Territory (Bowman et al., 1991; Wilson et al.,

1991). These are categorised as 'wet' and 'dry' monsoon forests (Russell-Smith, 1991). Both categories show a relationship between environment and floristic composition. The wet forests, of interest here, are a mixed species monsoon vine-thicket or forest, with many plant species having a disjunct distribution with Queensland, New Guinea and Indonesia. Most of the tree species have large seeds which are probably dispersed in part by birds. This forest commonly occurs on permanently moist to wet alluvial soils in low relief landscapes. A distinct subtype of closed canopy forest is dominated by the tree *Allosyncarpia ternata* S.T. Blake (Myrtaceae) and such forests span a gradient from wet to dry climatic zones. Although the wet forest types occur mostly in small and disjunct patches, there is evidence that significant gene flow exists between patches in most species of trees via pollen or vertebrate-dispersed seeds (Russell-Smith & Lee, 1992). In contrast, the seeds of *A. ternata* are very poorly dispersed (Bowman, 1991).

ALLOSYNCARPIA FORESTS. *Allosyncarpia ternata* is a fire-sensitive evergreen sclerophyll tree with a very limited distribution. It is endemic to western Arnhemland and adjacent Kakadu NP, and is largely restricted to sheltered gorges and rugged rock-strewn terrain where it is protected from fire (Bowman, 1991). This tree dominates the closed-canopy rainforests in this sandstone terrain. The genus contains only this single species and its total distribution is 12–14°S and 132–134°30'E. *Allosyncarpia* forest constitutes 41% of all rainforest in N and NW Australia (Bowman, 2000). Its distribution and vegetational diversity is documented in Russell-Smith et al. (1993).

It has been suggested that this type of rainforest may be of ancient origin (Bowman, 2000). There are several lines of evidence for this idea. First, it occurs only on the western edge of the Arnhemland Plateau, which has continuously been a subaerial erosional landscape since the late Cretaceous. Second, phylogenetic relationships of *Allosyncarpia* are with genera occurring on land masses derived from Gondwanaland rift fragments (e.g. New Caledonia). This means that stocks ancestral to these genera were separated at least in the late Cretaceous (Russell-Smith et al., 1993). *Allosyncarpia* is significantly basal to the *Eucalyptus* clade, and *Allosyncarpia* forests are conceivably a relict of late Cretaceous and early

Tertiary Australian closed forests (Bowman, 2000).

Biogeographic history of these forests is poorly understood. Only at Riversleigh, Queensland (Archer et al., 1989) do we have direct data on Tertiary vertebrate and plant macrofossils of rainforest habitat in northern Australia. In contrast, there is fairly good plant macrofossil or palynological data elsewhere in Australia for the late Cretaceous, Tertiary and Pleistocene (Trusswell, 1990). The gross biogeographic history of N Australian forests has thus been reconstructed from scant indirect animal data and scant direct plant evidence.

The forest considered in this study is in a remote, deeply-incised E–W gorge in the catchment of the East Alligator River, 32.5 km E of Jabiru, 12°87'73"S, 133°26'73"E. The site contains more rare plant species and greater total species diversity of gymnosperms and angiosperms than any other site in the Northern Territory; it also has the largest population of an endemic, highly restricted, and undescribed conifer (*Podocarpus* sp.) (Russell-Smith et al., 1993). The site is commonly called 'Podocarpus Canyon'. The extreme spatial restriction of this *Podocarpus* and many other rare rainforest taxa strongly suggests that the site is a biotic refugium and that relictual invertebrates might be present.

As part of a study of beetle species diversity and distribution in 10 separate NT rainforests, the *Allosyncarpia ternata* forest refugium of Podocarpus Canyon was sampled in detail. Beetles were chosen because of their abundance and diversity in forest systems, and because their patterns may be characteristic of those of insects in general. The purpose of this report is to give results, analysis and interpretation of the beetles found at Podocarpus Canyon. The goal was to determine if any beetle species are endemic or disjunct in this forest, and if this part of the insect fauna has a distinctive relictual or refugial character. Broadly speaking, the question is: can beetles resolve questions about the historical and ecological biogeography of this ancient rainforest type, which is now relictual and restricted to a very limited area in the NT?

MATERIALS AND METHODS

A rare opportunity combining permits and logistic support from the Conservation Commission of the Northern Territory allowed placement of insect traps in Podocarpus Canyon on 15 December and their retrieval on 23

December, 1993. Beetles were sampled by standard methods; using ultra-violet light traps, a malaise trap, 60 unbaited pitfall traps and 6 flight intercept traps. Flight intercept traps are not yet widely known. They are 2m long black fabric screens into which beetles fly, and then fall into troughs or pans containing a glycol preservative (Peck & Davies, 1980). These are extremely productive and efficient sampling devices for crepuscular and nocturnal beetles, especially in the Staphylinioidea. The dense canopy of the forest eliminates herbaceous and shrub vegetation on the forest floor. Standard sampling of low vegetation by beating and sweeping in the forest understory was not possible.

Identifications of the beetles were by the author or taxonomic specialists. Voucher specimens are in the collections of the Australian National Insect Collection, Canberra and the The Canadian Museum of Nature, Aylmer, Quebec. Data on habitat preferences and distributions for named species were sought in taxonomic papers, Naumann et al. (1991) or the Zoological Catalogue of Australia.

Insects present several possible broad distributional patterns which may suggest the history of a particular forest. In Australia general patterns of Australian insect zoogeography are known (Cranston & Naumann, 1991) as are broad zoogeographic patterns of beetle distributions (Howden, 1981). The following criteria were applied in seeking species judged to be useful in a historical biogeographic context.

1) Beetle species that occur in both rainforest and eucalypt woodland can probably easily move between separate rainforest patches. These species are of little value for the present study. Species known only from rainforests are the ones that have information value for this study.

2) Species exclusive to rainforest and found in either or both Queensland and WA as well as NT forests and which are disjunct between these areas may suggest either (1) fragmentation of formerly continuous rainforest distributions, or (2) late Pleistocene-Recent dispersal, perhaps through now-vanished forest corridors. Flightless species are most likely to have low dispersal potential, and to be evidence of range fragmentation.

3) Species limited to NT rainforests with sister species in Queensland or WA rainforest may suggest a common or continuous distribution in late Tertiary or early Pleistocene time, and this distribution was severed, allowing formation of

the species pairs. Degree of differentiation between the pairs may be proportional to time of separation.

4) Unusual genera or phylogenetically relictual species may be indicative of a long period of isolation and of extinction of relatives, possibly caused by Tertiary-Pleistocene climatic change. It is necessary to differentiate between this and the possibility that the taxon is a relatively recent aerial arrival from the poorly known fauna of the Indo-Malay Archipelago.

RESULTS

DIVERSITY. A total of 58 families, and at least 318 genera and 508 species were taken. Most of the species are of small body size (5mm or less). Most of these proved to be in families and genera which are not yet taxonomically well studied in Australia in general, and in NT in particular. For most, only generic names could be determined (Appendix). Only 40 taxa could be named to species. These were generally species of larger body size, in the better known families such as Carabidae, Dytiscidae, and Scarabaeidae. Seven additional species were recognised as undescribed, and one of these has since been described (*Australoxenella wurrook* Storey & Howden, 1996). Undoubtedly a great many of the others, especially the smaller ones, are also undescribed species. These 47 recognised species are all generalist feeders, with no direct stenophagous association with individual plant species in the forest. No flightless species were found.

In terms of numbers of species and individual specimens, the most effective sampling methods were UV light traps (311 species and 3076 individuals) and flight intercept traps (215 species and 1418 individuals). Pit traps (27 species and 156 individuals) and malaise traps (23 species and 43 individuals) took an order of magnitude fewer species and individuals, but the sampling effort was not equivalent. All methods except malaise traps took species not sampled by other methods.

BIOGEOGRAPHIC PATTERNS. Forty seven species could be discriminated as named or new and are potentially informative. Of these, 35 were previously reported from NT, and 12 others of these were new species or species records for NT (Table 1). Thirty two species were previously known from Queensland, 16 from WA, 3 from New Guinea or the Oriental Region, and 11 with ranges into NSW or other states of Australia.

TABLE 1. Beetles from the *Allosyncarpia* rainforest in Podocarpus Canyon, Arnhemland, NT which could be identified to species, giving numbers of individuals by sampling method, and primary habitat and distribution data. A full list of all other taxa is in the appendix. Families according to Lawrence and Britton 1991, 1994. Column headings and abbreviations: Mal = malaise trap, Inter = flight intercept trap, Pit = unbaited pitfall trap, UV = uv light trap, Hab = known primary habitats for the species elsewhere: R = rainforest, S = open savannah woodlands; A = aquatic; Dist = distribution in other localities; NSW = New South Wales; NT = North Territory; NG = New Guinea and/or Oriental; Q = Queensland; WA = Western Australia; etc=additional states in Australia; * = new record for NT.

Taxon	Mal	Inter	Pit	UV	Hab	Dist
Suborder Adephaga						
Carabidae (data from Moore et al. (1987)						
<i>Chlaenius flaviguttatus</i> Macleay				1	R	NT, Q, etc
<i>Tachys</i> 'nervosus' Slade				1	R	NT, Q, WA
<i>Cratogaster sulcata</i> Blanchard		28			R	NT
<i>Lorostema bothriophora</i> (Redtenbacher)			24		R	NT
<i>Gnathaphanus whitei</i> Slade				4	R	NT, Q
<i>Pentagonica ruficollis</i> S.G.				8	R	NT, Q, NG
<i>Aephnidius adelioides</i> Macleay				1	R	NT*, WA, Q, NG
<i>Helluosoma atrum</i> Castelnau				2	R	NT, Q
<i>Holcorderus caeruleipennis</i> Slade				1	R	NT*, Q
Haliplidae (data from Lawrence et al. 1987, Larson 1994)						
<i>Haliplus australis</i> Clark				1	S	NT, Q, etc.
Dytiscidae (data from Lawrence et al. 1987, Larson 1994)						
<i>Bidessodes flavosignatus</i> (Zimm.)				1	S	NT, Q
<i>Clypeodytes bifasciata</i> Zimm.				5	S	NT, Q
<i>Clypeodytes migrator</i> (Sharp)				5	S	NT, Q, etc.
<i>Copelatus bakewelli</i> Balfour-Brown				59	S, R	NT, WA
<i>Copelatus clarki</i> Sharp				2	S, R	NT, Q
<i>Hydaticus daemeli</i> Sharp				2	S	NT, WA, Q
<i>Hydroglyphus godeffroyi</i> (Sharp)				3	S, R	NT, WA, Q
<i>Hydrovatus ovalis</i> Sharp				3	S	NT, Q
<i>Platynectes decempunctatus</i> (Fab.)				10	S, R	NT, WA, Q, etc.
<i>Platynectes monostigma</i> Hope				3	S	NT, WA, Q
Suborder Polyphaga						
Hydrophiloidea						
Hydrophilidae						
<i>Sternolophus australis</i> Watts				15	R, S	NT, WA, Q
<i>Sternolophus marginicollis</i> Hope				2	R, S	NT, WA, Q, etc.
Staphylinoidea						
Leiodidae						
<i>Colenisia</i> n. sp. 1		12	1	18	R	NT*
<i>Colenisia</i> n. sp. 2		1	1		R	NT*
<i>Colenisia</i> n. sp. 3				12	R	NT*
<i>Colon</i> n. sp.		7		4	R	NT*
<i>Zeadalopus</i> n. sp. 1		1			R	NT*
<i>Zeadalopus</i> n. sp. 2		4			R	NT*
Staphylinidae: Pselaphinae						
<i>Eudranes carinatus</i> Sharp		1			R, S	NT
Scarabaeiformia						
Scarabaeoidea (data from Houston 1992, Storey & Howden 1996)						
Lucanidae						
<i>Figulus regularis</i> Westwood			1		R	NT, WA, Q

TABLE 1 (Cont.)

Taxon	Mal	Inter	Pit	UV	Hab	Dist
Geotrupidae						
<i>Australobolbus rotundatus</i> (Hope)				1	R, S	NT, Q, NG
Hybosoridae						
<i>Liparochrus infantus</i> Petrovic				13	R, S	NT, Q
<i>Lipchrus quadrimaculatus</i> Harold				1	R	NT, Q
Scarabaeidae						
<i>Ataenius occidentalis</i> (Macleay)				8	R, S	NT*, WA
<i>Aphodopsammobius rugicollis</i> (Macleay)		2			R, S	NT*, WA
<i>Coptodactyla lesnei</i> Paulian		32	5	63	R, S	NT
<i>Onthophagus latro</i> Harold				2	R, S	NT, Q
<i>Australoxenella wurrook</i> Storey & Howden	8				R	NT*
<i>Epholcis uniformis</i> Britton				1	R, S	NT
<i>Anoplostethus roseus</i> Blanchard				31	R	NT, Q
<i>Cryptodus obscurus</i> Macleay				1	R, S	NT*, Q, etc.
Coccinellidae						
<i>Scymnus mitior</i> Blackburn					R, S	NT, WA, Q, etc
Tenebrionoidea						
Archeocrypticidae (data from Kaszab, 1984)						
<i>Australenneboeus analis</i> (Kaszab)				2	R, S	NT, Q, etc
Tenebrionidae						
<i>Tanychilus pulcher</i> Carter				1	R, S	NT, WA, Q
Curculionoidea						
Brentidae						
<i>Schizoeupsalis promissus</i> (Pascoe)				2	R, S	NT, Q, etc
Curculionidae: Scolytinae (data from Wood & Bright, 1992)						
<i>Coccotrypes ductyliperda</i> (Fabricius)		10	4	18	R, S	NT, WA, Q, etc.
<i>Xyleborus perforans</i> (Wollaston)			7	3	R, S	NT, WA, Q, etc.

Of 47 potentially informative species, 28 are known to occur in savanna habitats and are thus uninformative for this study. The remaining 19 species are known only from rainforest habitat. Of these, 9 are known only from NT, 10 also occur in Queensland, 3 also occur in WA, 2 in New Guinea, and 1 has a range extending into NSW or other states. These distributions most parsimoniously suggest ranges achieved by random dispersal in the Recent, from a centre of greatest diversity in Queensland. Of the 9 species known only from NT rainforests, their sister species are not known, and morphologically none seem to be phylogenetic relicts.

DISCUSSION

DIVERSITY. Darwin-Kakadu insect faunas have been the focus of previous studies (Britton, 1973; Kikkawa & Monteith, 1980) allowing Baehr (1992) to state that hygrophilous carabid

beetles of N Australian refugia are as rich in Arnhemland as in N Queensland.

Naumann et al. (1991) reported 50 families, 191 genera, and 505 species of beetles from 8 Kimberley rainforest patches. Those results are difficult to compare with my study because samples were made in the dry season and by methods additional to those used here. A maximum of only 78 beetle species were found in the richest single forest patch. The rainforests and adjacent savanna forests yielded a shared fauna of 35 families, 134 genera, and 250 species of beetles. The fauna exclusive to the savanna forests was 51 families, 235 genera, and 433 species of beetles. Thus, the savanna beetle fauna of the Kimberley in the dry season was appreciably more diverse than that of the rainforests. This is counter to generalisations that the highest species diversity occurs in rainforest habitats. Mares (1992) indicated that Neotropical mammal species diversity is also greatest in

dryland habitats. I know of no comparative studies on diversity of Australian tropical savanna insects, but Andersen & Lonsdale (1990) eloquently elaborated on the importance of insects as the dominant herbivores in structuring the dynamics of Australian savannas.

In comparison to Kimberley rainforest patches, the beetle fauna of Podocarpus Canyon is apparently much more diverse. All Kimberley rainforest patches combined were species poorer than Podocarpus Canyon, but the sampling seasons were different. If the diversity of Podocarpus Canyon is less or comparable to that of the continuously humid rainforests of eastern Queensland is not yet known. No analysis is available for a Queensland rainforest beetle fauna for comparison. It is also not known to what extent the Podocarpus Canyon fauna is typical of NT rainforests in general or how it differs from that in adjacent savanna.

In a detailed species-level study on a part of the insect fauna of an NT rainforest patch, Andersen & Reichel (1994) found ants in Holmes Jungle, near Darwin, to be a more specialised rainforest fauna than that found in Kimberley rainforest patches. In NT rainforest ants in general, with 173 species in 46 genera, 27% are rainforest specialists, and some of these show distributional disjunctions, but none are endemic to NT rainforests (Reichel & Anderson, 1996). They also reported *Aphaenogaster* sp. B as unique to Podocarpus Canyon but this has since been found to be *Aphaenogaster pythia* Forel, a common Queensland species (Anderson pers. comm.).

It is frequently generalised that beetles may comprise 20–25% of the animal species diversity of any temperate or tropical terrestrial locality (Grove & Stork, 2000). Thus, Podocarpus Canyon, with over 500 beetle species, may possess as a minimum a total of 2000 insect species in the entire forest. In an elaborate and extensive study, Bassett & Arthington (1992) found 916 species of arthropods in 46000 specimens collected in flight intercept traps in the crowns of one species of rainforest tree in a 2 year study in N Queensland. The species were predominantly phytophagous. Ground dwelling and low-flying predators and scavengers were poorly represented. Davies & Margules (2000) reported 669 beetle species taken over several years in pittraps in eucalypt forests near Wog Wog, NSW. Allison et al. (1993) found 633 beetle species from 54 families by fogging 8 trees at 3 study sites in Papua New Guinea. These data

support an estimate of a minimum diversity of 2000 insect species in the Podocarpus Canyon rainforest patch.

BIOGEOGRAPHY. Various studies have attempted to understand the biogeographic history of Australian forests through the distribution of the forest inhabitants. These have concluded that NT rainforests must have been more extensive in the past, being progressively fragmented and reduced to their present status of very small, disjunct remnants. Menkhorst & Woinarski (1992) and Bowman & Woinarski (1994) found that various mammal species use NT rainforest at least occasionally, but that no species is restricted to it. The NT rainforest mammal species are like those of the monsoon rainforest of the Kimberley but unlike those of the wet tropical forest of Cape York. Likewise, the NT monsoon rainforests also contain few obligate species of herpetofauna and there is more species similarity with the Kimberley than with Cape York (Gambold & Woinarski, 1993).

There is no direct evidence that the beetle assemblage contains any relictual or ancient components. The indirect evidence of the wide and disjunct distribution of most of the named species could be used to bolster either dispersal or range fragmentation arguments. The history of climatic change in NT and elsewhere in Australia in Pleistocene times is a dynamic one of alternating dry (glacial) and wet (interglacial) climates (Johnson et al., 1999). Porch & Elias (2000) summarised that these have sponsored many range shifts in beetles in Australia, but that distributional details and fossil documentation is lacking. Baeher (1992) accounted for the assembly of a rich diversity of hygrophilous carabid beetles in Arnhemland refugia through this mechanism of climatic change causing repeated range expansion and contraction.

CONCLUSIONS

A diverse beetle fauna inhabits the *Allosyn- carpia* forest of Podocarpus Canyon. This study was able to segregate 58 families, and at least 318 genera and 508 species in samples of 4756 individual beetles. In spite of previous survey and taxonomic work, the beetle fauna of NT rainforests is still poorly known. Species level identifications were not generally possible. Few species could be named and their habitat preferences and distributions were not well enough known to be of use in constructing a numerically significant database for rigorously

evaluating distributional patterns useful in interpreting past history of the forests. Whether or not phylogenetic and distributional patterns presented by a beetle fauna can contribute to understanding of the history of these forests is not yet evident.

Available evidence favors the interpretation that the *Allosyncarpia* rainforests are, in general, not static biotic assemblages which have remained relatively constant through long periods of time, but rather that they are dynamic plant assemblages. The present rainforest patches were formed through time by dispersal in a dynamic landscape shaped by climatic change, erosional deposition, and water table fluctuation (which is ultimately controlled by sea level) (Bowman, 2000). These processes have created a changing landscape in which conditions for the establishment of rainforest come and go through time. In light of this study and subjective impressions from fieldwork in other NT rainforests, I conclude that NT rainforest beetle faunas are fortuitous and changing assemblages. As such they will shed little light on understanding the history of the forests. Of more use will be actual beetle fossils and subfossils, which have proved to be so informative in interpreting Quaternary habitat change in north temperate countries (Porch & Elias, 2000). However, the extreme environment of NT is generally unfavorable for the preservation of such fossils.

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LITERATURE CITED

- ALLISON, A. SAMUELSON, G.A. & MILLER, S.E. 1993. Patterns of beetle species diversity in New Guinea rainforest as revealed by canopy fogging: preliminary findings. *Selbyana* 14: 16-20.
- ANDERSON, A.N. & LONSDALE, W.M. 1990. Herbivory by insects in Austalian tropical savannas: a review. *Journal of Biogeography* 17: 433-444.
- ANDERSON, A.N. & MJER, J.D. 1991. The structure and biogeography of rainforest ant communities in the Kimberley region of northwestern Australia. Pp. 333-346. In McKenzie N.L., Johnston, R.B. & Kendrick, P.G. (eds) *Kimberley rainforests*. (Surrey, Beatty & Sons: Chipping Norton).
- ANDERSON, A.N. & REICHEL, H. 1994. The ant (Hymenoptera: Formicidae) fauna of Holmes Jungle, a rainforest patch in the seasonal tropics of Australia's Northern Territory. *Journal of the Australian Entomological Society* 33: 153-158.
- ARCHER, M., GODTHELP, H., HAND, S.J. & MEGIRIAN, D. 1989. Fossil mammals of Riversleigh, northwestern Queensland: preliminary overview of biostratigraphy, correlation and environment change. *Australian Zoologist* 25: 29-65.
- BAEHR, M. 1992. An introduction to the biogeography of the Carabidae of montane refugia in Northern Australia (Coleoptera: Carabidae). Pp. 67-78. In Noonan, G.R. Ball, G.E. & Stork N.E. (eds) *The biogeography of ground beetles of mountains and islands*. (Intercept: London).
- BASSET, M.T. & ARTHINGTON, A.H. 1992. The arthropod community of an Australian rainforest tree: abundance of component taxa, species richness and guild structure. *Australian Journal of Ecology* 17: 89-98.
- BOWMAN, D.M.J.S. 1991. Environmental determinants of *Allosyncarpia ternata* forests that are endemic to western Arnhemland, northern Australia. *Australian Journal of Botany* 39: 575-589.
- BOWMAN, D.M.J.S. 2000. *Australian rainforests: islands of green in a land of fire*. (Cambridge University Press: New York).
- BOWMAN, D.M.J.S., WILSON, B.A. & McDONOUGH, L. 1991. Monsoon forests in northern Australia. 1. Vegetation classification and the environmental control of tree species. *Journal of Biogeography* 18: 679-686.
- BOWMAN, D.M.J.S. & WOINARSKI, J.C.Z. 1994. Biogeography of Australian monsoon rainforest mammals: implications for the conservation of rainforest mammals. *Pacific Conservation Biology* 1: 98-106.

- BRITTON, E.B. 1973. Appendix 6, Coleoptera. In: Alligator Rivers region environmental fact-finding study. (Unpubl. report) (Entomology, CSIRO: Canberra)
- CRANSTON, P.S. & NAUMANN, I.D. 1991. Biogeography. Pp. 180-197. In CSIRO (ed.) *Insects of Australia*. Vol. 1 (Melbourne University Press: Carlton).
- DAVIES, K.F. & MARGULES, C.R. 2000. The beetles at Wog Wog: a contribution of Coleoptera systematics to an ecological field experiment. *Invertebrate Taxonomy* 14: 953-958.
- GAMBOLD, N. & WOINARSKI, J.C.Z. 1993. Distributional patterns of herpetofauna in monsoon rainforests of the Northern Territory, Australia. *Australian Journal of Ecology* 18: 431-449.
- GROVE, S.J. & STORK, N.E. 2000. An inordinate fondness for beetles. *Invertebrate Taxonomy* 14: 733-739.
- HOUSTON, W.W.K. (ed.) 1992. *Zoological catalogue of Australia*. Vol. 9. Coleoptera: Scarabaeoidea. Pp. XII-544. (Australian Government Publishing Service: Canberra).
- HOWDEN, H.F. 1981. Zoogeography of some Australian Coleoptera as exemplified by the Scarabaeoidea. Pp. 1009-1035. In Keast, A. (ed.) *Ecological biogeography of Australia*. (W. Junk: The Hague).
- JOHNSON, B.J., MILLER, G.H., FOGEL, M.L., MAGEE, J.W., GAGAN, M.K. & CHIVAS, A. R. 1999. 65,000 years of vegetation change in central Australia and the Australian summer monsoon. *Science* 284: 1150-1152.
- KASZAB, Z. 1984. Revision des australischen Archeocrypticinen (Coleoptera, Tenebrionidae). *Annales Historico-naturales Musei Nationalis Hungarici* 76: 143-163.
- KIKKAWA, J. & MONTEITH, G.B. 1980. Animal ecology of monsoon forests of the Kakadu region, Northern Territory. (A consultancy report to the Director, Australian National Parks and Wildlife, Canberra, ACT)
- KIKKAWA, J., WEBB, L.J., DALE, M.B., MONTEITH, G.B., TRACEY, J.G. & WILLIAMS, W.T. 1981. Gradients and boundaries of monsoon forests in Australia. *Proceedings of the Ecological Society of Australia* 11: 39-52.
- LARSON, D.J. 1994. Ecology of tropical Hydradephaga (Insecta: Coleoptera). Part I. Natural history and distribution of northern Queensland species. *Proceedings of the Royal Society of Queensland* 103: 47-63.
- LAWRENCE, J.F. & BRITTON, E.B. 1991. Coleoptera. Pp. 543-683. In CSIRO (ed.) *Insects of Australia*. Vol. 2. (Melbourne University Press: Carlton).
1994. *Australian beetles*. (Melbourne University Press: Carlton).
- LAWRENCE, J.F., WEIR, T.A. & PYKE, J.E. 1987. Haliplidae, Hygrobiidae, Noteridae, Dytiscidae, and Gyrinidae. Pp. 321-366. In *Zoological catalogue of Australia*. Vol. 4. Coleoptera: Archostemata, Myxophaga, and Adephaga. (Australian Government Publishing Service: Canberra).
- MAJER, J.D. 1990. The abundance and diversity of arboreal ants in Northern Australia. *Biotropica* 22: 191-199.
- MARES, M.A. 1992. Neotropical mammals and the myth of Amazonian biodiversity. *Science* 255: 976-979.
- MENKHORST, K.A. & WOINARSKI, J.C.Z. 1992. Distribution of mammals in monsoon rainforests of the Northern Territory. *Wildlife Research* 19: 295-316.
- MOORE, B.P., WEIR, T.A. & PYKE, J.E. 1987. Rhysodidae and Carabidae. Pp. 17-320. In *Zoological catalogue of Australia*. Vol. 4 Coleoptera: Archostemata, Myxophaga, and Adephaga. (Australian Government Publishing Service: Canberra).
- NAUMANN, I.D., WEIR, T.A. & EDWARDS, E.D. 1991. *Insects of Kimberley Rainforests*. Pp. 299-332. In McKenzie, N.L., Johnson, R.B. & Kendrick, P. G. (eds) *Kimberley rainforests of Australia*. (Surrey Beatty & Sons: Chipping Norton).
- PECK, S.B. & DAVIES, A. 1980. Collecting small beetles with large area window traps. *Coleopterists Bulletin* 34: 237-239.
- PORCH, N. & ELIAS, S. 2000. Quaternary beetles: a review and issues for Australian studies. *Australian Journal of Entomology* 39: 1-9.
- REICHL, H. & ANDERSON, A.N. 1996. The rainforest ant fauna of Australia's Northern Territory. *Australian Journal of Zoology* 44: 81-95.
- RUSSELL-SMITH, J. 1991. Classification, species richness, and environmental relations of monsoon rainforest in northern Australia. *Journal of Vegetation Science* 2: 259-278.
- RUSSELL-SMITH, J. & LEE, A.H. 1992. Plant populations and monsoon rainforest in the Northern Territory, Australia. *Biotropica* 24: 471-487.
- RUSSELL-SMITH, J., LUCAS, D.E., BROCK, J. & BOWMAN, D.M.J.S. 1993. *Allosyncarpia*-dominated rainforest in monsoonal northern Australia. *Journal of Vegetation Science* 4: 67-82.
- STOREY, R.I. & HOWDEN, H.F. 1996. Revision of *Australoxenella* Howden & Storey in Australia (Coleoptera: Scarabaeidae: Aphodiinae). *Memoirs of the Queensland Museum* 39: 365-380.
- TRUSSWELL, E.M. 1990. Australian rainforests: the 100 million year record. Pp. 7-22. In Webb L.J. & Kikkawa, J. (eds) *Australian tropical rainforests: science-values-meaning*. (CSIRO: Melbourne).
- WILSON, B.A., BROCKLEHURST, P.S., CLARK, M.J. & DICKINSON, K.J.M. 1991. Vegetation survey of the Northern Territory, Northern map sheet and technical report 49. (Conservation Commission of the Northern Territory: Palmerston).
- WOOD, S. & BRIGHT, D. 1992. A catalog of Scolytidae and Platypodidae (Coleoptera), part 2: taxonomic index volumes A & B. *Great Basin Naturalist Memoirs* 13: 1553.

APPENDIX

Taxa and numbers of all individuals of beetles which could not be placed to named or new species category, found in *Allosyncarpia* rainforest in Podocarpus Canyon, Arnhemland, NT, by sampling method. Families according to Lawrence & Britten, 1991, 1994. Column headings and abbreviations: Mal = malaise trap, Inter = flight intercept trap, Pit = unbaited pitfall trap, UV = uv light trap.

Taxon	Mal	Inter	Pit	UV
Suborder Adephaga				
Carabidae (classification follows Moore et al. (1987)				
Callistitae				
<i>Badister</i> sp.				4
Scarititae				
<i>Clivina</i> sp. 1				1
<i>Clivina</i> sp. 2				2
<i>Dischirius</i> sp.				5
Trechitae				
<i>Limnastis</i> sp.				1
<i>Tachys</i> s.lat. sp. 1	1			
<i>Tachys</i> s.lat. sp. 2				2
<i>Tachys</i> s.lat. sp. 3				9
<i>Tachys</i> s.lat. sp. 4				31
<i>Tachys</i> s.lat. sp. 5				3
<i>Tachyta</i> sp.				5
<i>Tachyninia</i> genus sp.				3
<i>Trechodes</i> sp.				1
Pterostichitae				
<i>Abacetis</i> sp.				1
<i>Loxandrus</i> sp.				2
<i>Morton</i> sp.				1
<i>Prosopogmus</i> sp.				7
Perigonitae				
<i>Perigona</i> sp.				85
Harpalitae				
<i>Acupalpus</i> sp.				1
gen. 2, sp.				2
gen. 3, sp.				9
<i>Hypharpax</i> sp.				1
<i>Notiobia</i> sp.				2
<i>Trichotichnus</i> sp.				1
Oodini				
<i>Coptocarpus</i> sp.				1
Pentagonitae				
<i>Pentagonica</i> sp.			1	15
Masoreitae				
<i>Sarothrocrepis</i> sp.				3
Lebiitae				
<i>Agonocheila</i> sp.				1
<i>Anomotarus</i> sp.			1	14
<i>Helluodema</i> sp.				
<i>Minuthodes</i> sp.				2
<i>Parazuphium</i>				1
<i>Pogonoglossus</i> sp.				2
<i>Trigonothops</i> sp.				4
Noteridae (classification from Lawrence et al. 1987, Larson 1994)				
<i>Canthydrius</i> sp. (new?)			5	
<i>Hydrocoptus</i> sp. (new?)			1	
Dytiscidae (classification from Lawrence et al. 1987, Larson 1994)				
<i>Clypeodytes</i> n.sp.			1	
<i>Copelatus</i> n.sp.			1	

Taxon	Mal	Inter	Pit	UV
Suborder Polyphaga				
Staphyliniformia				
Hydrophiloidea				
Hydrophilidae				
<i>Anacaena</i> sp.1			20	
<i>Anacaena</i> sp.2			14	
<i>Berosus</i> sp.			5	
<i>Enochrus?</i> sp.1			1	
<i>Enochrus</i> sp.2			1	
<i>Enochrus</i> sp.3			8	
<i>Georissus</i> sp.			11	
<i>Globaria?</i> sp.			1	
<i>Helochaeres</i> sp.1			2	
<i>Helochaeres</i> sp.2			6	
<i>Hydrochus</i> sp.			50	
<i>Paracymus</i> sp.			1	
<i>Sperchus</i> sp.			1	
<i>Sphaeridinae</i> gen.1 sp.1	2	1	4	
<i>Sphaeridiinae</i> gen.1 sp.2			1	
Histeridae				
nr. <i>Chlamydopsis</i> (<i>termitophilus</i>)		1		
Staphylinoidae				
Hydraenidae				
genus 1		2		151
Ptiliidae				
unsorted			61	
Scydmaenidae				
<i>Coatesia</i> sp.		1		
Genus 1 sp.1		115		6
Genus 1 sp.2		27		1
Genus 1 sp.3		32		59
Genus 1 sp.4		5		2
Genus 1 sp.5		5		3
Genus 1 sp.6		14		43
Genus 1 sp.7		5		15
Staphylinidae				
Tachyporinae				
<i>Sepedophilus</i> ; 2 spp.				3
Aleocharinae				
<i>Mesoporini</i> gen. & sp.				1
<i>Myllaena</i> sp.		1		1
16 genera; 22 spp.			1	88
13 genera; 18 spp.				68
Osoriinae				
<i>Osorius</i> sp.				5
Oxytelinae				
<i>Bledius</i> ; 7 spp.		22		271
<i>Carpelimus</i> ; 7 spp.		44		60
<i>Thinobius</i> ; 2 spp.				3
<i>Thinodromus</i> sp.		1		
<i>Anotylus</i> ; 3 spp.		1		42
Euaesthetinae				
<i>Edaphus</i> ; 2 spp.		6		5

Taxon	Mal	Inter	Pit	UV
Paederinae				
<i>Cephalochetus</i> sp.				3
<i>Charichirus</i> sp.		1		4
<i>Dibelonetes</i> sp.		1		
<i>Lathrobium</i> , 2 spp.				3
<i>Lithocharis</i> sp.			1	
<i>Ochtheophilum</i> , 3 spp.				22
<i>Pinobius</i> sp.				2
<i>Scopaeodracus</i> sp.				3
<i>Scopaeus</i> , 2 spp.	1		6	
<i>Stiliderus</i> sp.	1			
<i>Sunius</i> , 2 spp.		11		5
<i>Thinoharis</i> sp.	1		1	
<i>Oedichirus</i> sp.				1
<i>Palaminus</i> sp.		1		
<i>Pinophilus</i> , 3 spp.				13
Staphylininae				
<i>Diachus</i> , 2 spp.		5		2
<i>Hesperus</i> sp.	1	100	8	9
<i>Philonthus</i> sp.				1
<i>Acylophorus</i> sp.			3	
<i>Atanygnathus</i> sp.	1		1	
Scaphidiinae				
<i>Scaphisoma</i> sp.	7		2	
<i>Baeocera</i> sp. 1		3		
<i>Baeocera</i> sp. 2		3		
<i>Scaphobaeocera</i> sp. 1		18		
<i>Scaphobaeocera</i> sp. 2		5		
Pselaphinae				
<i>Bibloporellina</i> n.gen.		7		
<i>Brachyglutina</i> n.gen. #1	4			
<i>Brachyglutina</i> n.gen. #3	1			
<i>Brachyglutina</i> n.gen. #5	1			
<i>Brachyglutina</i> n.gen. #6	1			
<i>Bythinoplectini</i> gen? #1	18			
<i>Bythinoplectini</i> gen? #2	1			
<i>Bythinoplectini</i> gen? #3	1			
<i>Bythinoplectini</i> gen? #4	1			
<i>Bythinoplectini</i> gen? #5	1			
<i>Bythinoplectini</i> gen? #6	1			
<i>Clavigeropsis</i> sp. 1		1		
<i>Clavigeropsis</i> sp. 2		46		
<i>Clavigeropsis</i> sp. 3		1		
<i>Coryphomodes</i> sp. 1		1		
<i>Coryphomodes</i> sp. 3		4		
<i>Curculionellus</i> sp. 2		4		
<i>Curculionellus</i> sp. 5		1		
<i>Cyathiger</i> sp. 1	7			
<i>Durbos</i> sp. 1		8		
<i>Eupines</i> sp. 1		2		
<i>Eupines</i> sp. 3		1		
<i>Eupines</i> sp. 4		1		
<i>Eupines</i> sp. 5		2		
<i>Eupines</i> sp. 6		1		
<i>Eupines</i> sp. 7		1		
<i>Eupines</i> sp. 8		2		
<i>Eupines</i> sp. 10		1		
<i>Eupines</i> sp. 11		1		
<i>Eupines</i> sp. 13		1		
<i>Eupines</i> sp. 14		3		
<i>Eupines</i> sp. 15		1		

Taxon	Mal	Inter	Pit	UV
<i>Euplectini</i> gen. #4		35		
<i>Euplectini</i> gen. B	1			
<i>Euplectini</i> gen. C	1			
<i>Euplectus</i> sp. 1	4			
<i>Euplectus</i> sp. 2	1			
<i>Euplectus</i> sp. 3	1			
<i>Euplectus</i> sp. 4	2			
<i>Limoniates</i> sp. 1	5			
<i>Limoniates</i> sp. 2	10			
nr. <i>Eupines</i> sp. 1	53			
nr. <i>Eupines</i> sp. 2	1			
nr. <i>Eupines</i> sp. 3	116			
nr. <i>Mesoplatus</i> sp. 1		2		
<i>Palimbohus</i> sp. 1	1			
<i>Palimbohus</i> sp. 2	2			
<i>Pselaphaulax</i> sp. 1		1		
<i>Pselaphaulax</i> sp. 2		3		
<i>Pselaphaulax</i> sp. 7		21		
<i>Pselaphaulax</i> sp. 10		1		
<i>Pselaphaulax</i> sp. 12		3		
<i>Pselaphaulax</i> sp. 13		2		
<i>Pselaphaulax</i> sp. 14		5		
<i>Pselaphaulax</i> sp. 15		6		
<i>Tiracerus</i> sp. 1	2			
<i>Tiracerus</i> sp. 2	1			
<i>Tmesiphorus</i> sp. 1		2		
<i>Tmesiphorus</i> sp. 3		1		
<i>Tmesiphorus</i> sp. 4		4		
<i>Tmesiphorus</i> sp. 5		1		
<i>Tyraphus</i> sp. 4		5		
<i>Tyraphus</i> sp. 5		1		
Scirtiformia				
Scirtoidea				
Scirtidae				
<i>Cyphon</i> sp.1		44		
<i>Cyphon</i> sp.2		4		15
<i>Cyphon</i> sp.3				1
<i>Scirtes</i> sp.1		1		
Eucinetidae				
<i>Eucinetus</i> sp.	1	17		19
Clambidae				
<i>Clambus</i> sp.		25		
Scarabaeiformia				
Scarabaeoidea (data from Houston 1992)				
Scarabaeidae				
Aphodiinae				
Eupariini				
<i>Australammoeius</i> sp.			1	1
Coprini				
<i>Demarziella</i> sp.		1		
Onthophagini				
<i>Onthophagus</i> sp.1		1		
<i>Onthophagus</i> sp.2			2	
<i>Onthophagus</i> sp.3				1
<i>Onthophagus</i> sp.4				1
<i>Onthophagus</i> sp.5		1		
Scarabaeini				
<i>Lepanus</i> sp.1		6		
<i>Lepanus</i> sp.2		1		
<i>Sauvagesenella</i> sp.				1

Taxon	Mal	Inter	Pit	UV
Melolothinae				
Automoliini				
<i>Haploopsis</i> sp.2				4
Liparetrini				
<i>Colpochila</i> sp.				1
<i>Liparetrus</i> sp.				1
Heteronycini				
<i>Heteronyx</i> sp. 1				21
<i>Heteronyx</i> sp. 2				1
<i>Heteronyx</i> sp. 3				2
<i>Heteronyx</i> sp. 4				3
<i>Heteronyx</i> sp. 5				1
<i>Heteronyx</i> sp. 6				27
<i>Heteronyx</i> sp. 7	1	6		81
<i>Heteronyx</i> sp. 8	1	2	1	3
<i>Heteronyx</i> sp. 9				12
<i>Heteronyx</i> sp. 10				2
<i>Heteronyx</i> sp. 11				1
<i>Heteronyx</i> sp. 12				6
<i>Heteronyx</i> sp. 13				11
<i>Heteronyx</i> sp. 14				1
<i>Heteronyx</i> sp. 15				5
<i>Heteronyx</i> sp. 16				1
<i>Heteronyx</i> sp. 17				3
<i>Neoheteronyx</i> sp.				3
Maechidiini				
<i>Maechidius</i> sp.	1	2		312
Melolonthini				
<i>Lepidiota</i> sp.1				4
<i>Lepidiota</i> sp.2				3
Genus 17				5
Elateriformia				
Byrrhoidea				
Limnichidae				
<i>Byrrhinus</i> sp. 1		1	1	105
<i>Byrrhinus</i> sp. 2				10
<i>Byrrhinus</i> sp. 3				5
' <i>Limnichus</i> ' sp. 1		1	1	7
' <i>Limnichus</i> ' sp. 2				5
Callirhipidae				
genus 1	3			34
Elateroidea				
Eucnemidae				
genus 1				1
genus 2				3
Throscidae				
<i>Aulonthroscus</i> sp. 1	1			1
<i>Aulonthroscus</i> sp. 2		1		
<i>Aulonthroscus</i> sp. 3		4		
Elateridae				
<i>Agrypnus</i> sp. 1				1
<i>Agrypnus</i> sp. 2				4
<i>Agrypnus</i> sp. 3				4
nr. <i>Antoligostethus</i> sp.				12
<i>Augentos</i> sp.				5
<i>Conoderus</i> sp. 1		9	1	
<i>Conoderus</i> sp. 2	8	7		
<i>Conoderus</i> sp. 3				16
<i>Conoderus</i> sp. 4				3
<i>Conoderus</i> sp. 5				3
<i>Conoderus</i> sp. 6				3

Taxon	Mal	Inter	Pit	UV
<i>Conoderus</i> sp. 7	1			
<i>Paracardiophus</i> sp.				20
<i>Melanoxanthus</i> sp. 1	2			167
<i>Melanoxanthus</i> sp. 2	1			
<i>Melanoxanthus</i> sp. 3				1
<i>Pseudotetralobus</i> sp.				6
genus 5		1		14
Lycidae				
genus 1 sp. 1				3
genus 1 sp. 2				3
genus 1 sp. 3				3
Lampyridae				
<i>Pteroptyx</i> ?sp.				3
Cantharidae				
genus 1 sp. 1				1
genus 2 sp. 1				3
Bostrichoidea				
Bostrichidae				
<i>Xylobosca</i> sp.				1
Anobiidae				
<i>Dorcatoma</i> sp. 1	1			1
<i>Gastrallus</i> sp.				4
<i>Pronus</i> ? sp.				1
Cleroidea				
Trogossitidae				
<i>Neaspis</i> sp.		1		27
Cleridae				
<i>Stigmatium</i> sp.		1		
genus 2 sp. 1				2
Cucujoidea				
Sphindidae				
<i>Aspidiphorus</i> sp.	2			
Nitidulidae				
<i>Carpophilus</i> sp. 1	1			
<i>Carpophilus</i> sp. 2	1			
<i>Cybocephalus</i> sp.	2			
<i>Lasiodactylus</i> sp.		3	33	
<i>Pallodes</i> sp.			6	
<i>Stelidota</i> sp.		96	76	
<i>Thylacrodes</i> sp.	1		18	
genus 8			1	
Silvanidae				
<i>Psammoecus</i> sp.	4		1	
<i>Silvanolomus</i> sp.			1	
Laemophloeidae				
<i>Placonotus</i> sp.				1
Phalacridae				
<i>Litochrus</i> sp. 1	1			
<i>Litochrus</i> sp. 2				1
<i>Litochrus</i> sp. 3				4
Languriidae				
<i>Cryptophilus</i> sp.			99	
Erotylidae				
<i>Episcaphula</i> sp. 1			3	
<i>Episcaphula</i> sp. 2			12	
<i>Thallis</i> sp.				1
Bothrideridae				
genus 1			1	
Cerylonidae				
<i>Cerylonopsis</i> sp. 1		3		3
<i>Cerylonopsis</i> sp. 2		1		27

Taxon	Mal	Inter	Pit	UV
Endomychidae				
<i>Holopatameans</i> sp. 1				5
Corylophidae				
<i>Anisomeristes</i> sp.	23		11	
<i>Lewisium?</i> sp.		2		1
<i>Orthoperus</i> sp.	7			
<i>Sericoderus</i> sp.	15			
genus 5	2			
genus 6	8			
genus 7	5			
genus 8			1	
Lathridiidae				
<i>Corticaria</i> sp. 1	1	5		54
<i>Corticaria</i> sp. 2				5
Tenebrionoidea				
Mycetophagidae				
<i>Litargus</i> sp. 1	6	3		8
Ciidae				
<i>Acanthocis</i> sp. 1	1			
<i>Cis pacificus</i> group		1		
Mordellidae				
<i>Glipostenoda?</i> sp.	5	3		15
<i>Mordellistena</i> sp.			6	
<i>Zeamordella?</i> sp.	1			
genus 4			4	
Colydiidae				
<i>Bolcocius</i> sp.				6
Tenebrionidae				
Tenebrioninae				
<i>Ectyche</i> sp.			1	
<i>Mesomorplus</i> sp.			1	
<i>Platydemia</i> sp. 1			4	
<i>Platydemia</i> sp. 2			3	
<i>Platydemia</i> sp. 3			2	
<i>Platydemia</i> sp. 4			1	
<i>Platydemia</i> sp. 5			2	
<i>Toxicum</i> sp.				1
<i>Uloma</i> sp.				5
genus 9			1	
Alleculinae				
nr. <i>Homotrysis</i> sp.				1
<i>Nocar</i> sp.		24	1	9
genus 1	7	3	15	
genus 3			3	
genus 4			1	
genus 5			6	
genus 6			1	
genus 8, unusual, claw not pectinate				2
Lagriinae				
<i>Casonidea</i> sp.			1	
Salpingidae				
<i>Lissodema?</i> sp.			1	
Anthicidae				
<i>Anthicus</i> sp. 1				3
<i>Anthicus</i> sp. 2				1
<i>Anthicus</i> sp. 3				1
<i>Anthicus</i> sp. 4				1

Taxon	Mal	Inter	Pit	UV
<i>Anthicus</i> sp. 5				3
<i>Anthicus</i> sp. 6				1
<i>Mecynotarsus</i> sp.			1	
Aderidae				
genus 1		1	2	
genus 2	1			
genus 3			1	
genus 4			2	
genus 5			1	
genus 6			5	
Scraptiidae				
<i>Scraptia</i> sp.				1
Chrysomeloidea				
Cerambycidae				
<i>Prosopius</i> sp.				1
Chrysomelidae				
<i>Geloptera</i> sp.				2
<i>Longitarsus</i> sp. 1	1			
<i>Longitarsus</i> sp. 2				1
<i>Monolepta</i> sp. 1	1			
<i>Monolepta</i> sp. 2	2			
<i>Monolepta</i> sp. 3				27
<i>Monolepta</i> sp. 4				12
<i>Pepila</i> sp.		1		
<i>Rhyarida</i> sp. 1	1			
<i>Rhyarida</i> sp. 2		1		78
<i>Trachyaphthona</i> sp.		1		
genus 4	1			
genus 12				3
Bruchinae				
<i>Callosobruchus</i> sp.				3
Curculionoidea				
Curculionidae				
Scolytinae (data from Wood & Bright, 1992)				
<i>Cryphalus</i> sp.				2
<i>Scolytomimus</i> sp.	1			
Cuculioninae				
genus 1	1	1	1	
genus 2	1	3		2
genus 3	1			5
genus 4	1			2
genus 5		3		
genus 6		1		
genus 7		4		
genus 8		1		
genus 9		1		
genus 12				3
genus 13				1
genus 14				1
Cossoninae				
genus 10		1		
genus 15				1
genus 16				1
Totals (including species data presented in Table 1):				
Number of species by sample method	23	215	27	311
Numbers of individuals by sample method	43	1,481	156	3,076
Totals: 58 families, minimally 318 genera, minimally 508 species				

PERAMELES SOBBEI SP. NOV. (MARSUPIALIA, PERAMELIDAE), A PLEISTOCENE BANDICOOT FROM THE DARLING DOWNS, SOUTH-EASTERN QUEENSLAND

GILBERT J. PRICE

Price, G.J. 2002 5 31: *Perameles sobbei* sp. nov. (Marsupialia, Peramelidae), a Pleistocene bandicoot from the Darling Downs, south-eastern Queensland. *Memoirs of the Queensland Museum* 48(1): 193-197. Brisbane. ISSN 0079-8835.

Perameles sobbei sp. nov. is described from Pleistocene fluvial sediments from King Creek on the eastern Darling Downs. *Perameles sobbei* falls within the size range of modern *Perameles* species, but its molar morphology indicates a closer affinity with the early Pliocene species, *P. bowensis*. Both species retain the plesiomorphic states of possessing straight cristid obliquas with closely approximated trigonid cuspids, and the synapomorphic state of the reduction of the hypoconulid on M₃. However, the great size difference and slight molar morphology differences between the two are considered sufficient to warrant specific separation. *Perameles sobbei* sp. nov. is the third fossil *Perameles* species described and the first from Pleistocene deposits. □ *Bandicoot, Perameles, Pleistocene, Darling Downs, King Creek.*

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Pleistocene fossils have been known from the eastern Darling Downs for over 160 years, with the first fossils collected by Sir Thomas Mitchell by 1842 (Owen, 1877). Recent faunal lists, such as that of Molnar & Kurz (1997), indicate a high degree of taxonomic diversity and wide distribution of Pleistocene vertebrates within the Darling Downs. Such lists are dominated by megafaunal species, notably mammals, in particular members of the Diprotodontidae, Vombatidae, Thylacoleonidae and Macropodidae, plus large reptiles from the Crocodylidae and Varanidae. Molnar & Kurz (1997) suggested that past collecting on the Darling Downs has been biased towards the recovery of larger specimens, thereby leading to an underestimation of the smaller vertebrate component.

Molnar & Kurz's (1997) view is supported by recent systematic collecting from an extensive fluvial deposit located 8 km W of Clifton along the banks of King Creek (Queensland Museum site L796). Along with representatives of the aforementioned Darling Downs megafaunal families, other vertebrate species recovered from this site include members of the Tachyglossidae, Ornithorhynchidae, Dasyuridae, Peramelidae and Muridae, plus Agamidae, Scincidae and Elapidae. Among the peramelids is a previously undescribed species of *Perameles*. To date, only two fossil species of *Perameles* have been described, both from Pliocene deposits: *P.*

allinghamensis from the Bluff Downs Local Fauna (Archer, 1976), and *P. bowensis* from the Bow, Big Sink (Muirhead et al., 1997) and Chinchilla Local Faunas (Mackness et al., 2000). *Perameles sobbei* sp. nov., is the first extinct species of the genus described from Pleistocene deposits.

Dental nomenclature follows Luckett (1993) where the adult unreduced cheek tooth formula of marsupials is P1-3 and M1-4 in both upper and lower dentitions. Tooth morphology nomenclature follows Freedman (1967). Some distinguishing features of *Perameles* follow those described by Smith (1972). Higher systematics follow Aplin & Archer (1987). Types are deposited in the Queensland Museum (QMF).

SYSTEMATIC PALAEOLOGY

Supercohort MARSUPIALIA Cuvier, 1817
Cohort AUSTRALIDELPHIA Szalay, 1982
Order PERAMELEMORPHIA Kirsch, 1968
Family PERAMELIDAE Gray, 1825

***Perameles* Geoffroy, 1804**

TYPE SPECIES. *Perameles nasuta* Geoffroy, 1804.

OTHER SPECIES. *Perameles bougainville* Quoy and Gaimard, 1824, *P. gunnii* Gray, 1838, *P. eremiana* Spencer, 1897; *P. allinghamensis* Archer, 1976; *P. bowensis* Muirhead, Dawson & Archer, 1997.

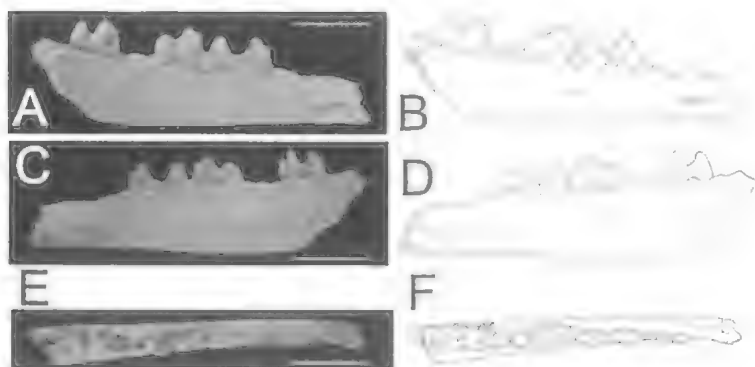


FIG. 1. *Perameles sobbei* sp. nov., holotype QMF43878, right dentary: A, B, buccal view; C, D, lingual view; E, F, occlusal view. Scale bars: 5mm.

***Perameles sobbei* sp. nov.**
(Figs 1, 2)

ETYMOLOGY. For Ian H. Sobbe of Clifton, for his contributions to Pleistocene faunas of the Darling Downs.

MATERIAL. HOLOTYPE: QMF43878 (Fig 1), portion of the horizontal ramus of a right dentary with P_2 - M_1 and M_3 . **PARATYPES:** QMF43879 (Fig. 2A, B), isolated right M_3 ; QMF43880 (Fig. 2C, D), isolated left M_4 . All types are from QML796, King Creek, E Darling Downs.

DIAGNOSIS. Hypoconulid reduced to absent on M_{1-3} ; M_1 long; M_3 narrow; M_4 talonid, markedly reduced in comparison to similar-sized species; trigonid cuspids equidistant; anterior cingulid on M_2 and M_3 prominent, rounded in its anterolingual corner.

DESCRIPTION. Dentary. Deepest below M_3 ; mandibular symphysis extending posteriorly to below P_1 ; mental foramen is anteroventral to anterior alveolus of the P_1 ; P_1 is missing, though length of its alveoli suggests premolars increase in size from P_1 to P_3 . M_4 is the shortest molar tooth, followed in ascending order by M_3 , M_1 and M_2 .

Right P_2 . Laterally compressed; sub-rectangular in occlusal outline, with slight lateral constriction one-third from anterior margin; anterior, central and posterior cuspids occupy midline of crown; central cuspid tallest and posterior cuspid shortest; central cuspid base in midline of tooth, though apex is curved lingually; wear facet present on posterior apex of central cuspid; abrasion from upper premolars has obscured any unique structures on posterior cuspid.

Right P_3 . Sub-rectangular in occlusal outline; anterior, central and posterior cuspids on crown;

central cuspid tallest and anterior cuspid shortest; anterior cuspid in lingual corner of tooth, its buccal surface sloping more gently towards crown base than does the lingual surface; central cuspid slightly lingual to midline, not curved lingually like corresponding cuspid of P_2 ; small blade-like crest running posteriorly along midline from apex of central cuspid to posterior extreme of posterior cuspid; horizontal shelf-like structure on lingual side of crest of posterior

cuspid extending anteriorly to posterolingual base of main cuspid; small shallow basin on horizontal shelf, positioned close to base of main cuspid; posterior cuspid slopes steeply to base of crown on buccal side of crest; faint ridge runs antero-posteriorly along longitudinal extent of the buccal sloped surface of posterior cuspid.

Right M_1 . Anterior one-third triangular, remainder rectangular in occlusal outline; talonid markedly wider than trigonid; metaconid taller than protoconid, both taller than paraconid; relative heights of hypoconid and entoconid indeterminable due to wear; paraconid forms anterior margin of tooth, positioned slightly lingual to midline; metaconid posterolingual to paraconid; protoconid occupies buccal portion of trigonid, slightly anterobuccal to metaconid; entoconid lies directly posterior to metaconid; hypoconid posterobuccal to protoconid; entoconid and hypoconid lie on same transverse plane; hypoconulid reduced to slight swelling at posterior base of entoconid; faint posthypocristid connects hypoconulid to hypoconid; form of cristid obliqua has been obliterated by wear; no anterior or posterior cingulid present.

Right M_2 . (Based on QMF43879, Fig. 2A, B); Anterior one-third triangular, remainder rectangular in occlusal outline; talonid markedly wider than trigonid; protoconid is tallest cuspid on crown, followed in descending order by metaconid, entoconid, hypoconid, and paraconid; paraconid is just posterior to anterior margin, positioned slightly lingual to midline; metaconid is posterolingual to paraconid; metaconid and protoconid are in same transverse plane; hypoconid is directly posterior to protoconid; entoconid is posterolingual to

metaconid; entoconid is lingual and slightly anterior to hypoconid; no hypoconulid is present; a faint posthypocristid runs posterolingually to posterior base of entoconid; cristid obliqua descends anterolingually from apex of hypoconid, curving slightly anteriorly to terminate at posterobuccal base of protoconid; anterior cingulid is low on the base of crown, rounded and bulbous in its lingual corner, tapering buccally to terminate at anterobuccal base of protoconid.

Right M₃. Sub-rectangular in occlusal outline; trigonid and talonid are of approximately equal width; metaconid is tallest cusp followed by protoconid then paraconid; comparison of heights of talonid cuspids to those of the trigonid not possible due to wear and broken posterior lingual corner of talonid; paraconid slightly posterior to anterior margin, positioned on lingual portion of tooth; metaconid directly posterior to paraconid; metaconid and protoconid are in same transverse plane; entoconid directly posterior to metaconid; hypoconid directly posterior to protoconid; entoconid and hypoconid are in the same transverse plane; hypoconulid reduced to a slight swelling at posterior base of entoconid; no posthypocristid present; cristid obliqua runs anterolingually from hypoconid curving slightly anteriorly to terminate lingual to midline of tooth at posterior base of metaconid; anterior cingulid positioned low on base of crown, rounded at its lingual corner, tapering buccally to terminate at anterobuccal base of protoconid.

Left M₄. (Based on QMF43880, Fig. 2C, D). Sub-rectangular in occlusal outline; trigonid wider than talonid; relative heights of cuspids indeterminable owing to wear, but trigonid cuspids are clearly taller than those of talonid; paraconid slightly posterior to anterior margin of tooth, positioned lingual to midline; metaconid posterolingual to paraconid; metaconid and protoconid are on same transverse plane; entoconid and hypoconid are closely approximated, positioned lingual to midline of tooth; talonid has been worn such that hypoconid and entoconid appear to be fused to form one main cuspid, however a slight constriction on apex suggests demarcation between very small entoconid and hypoconid cuspids; lingual corner of anterior cingulid is one half the way up anterior face of paraconid; anterior cingulid rounded and bulbous in lingual corner, descending buccally to terminate at anterobuccal base of protoconid,

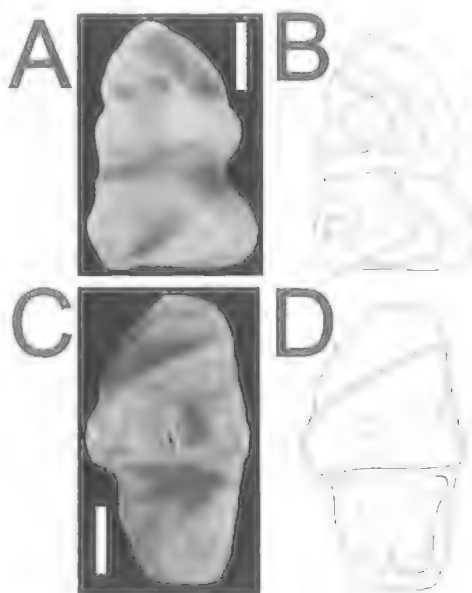


FIG. 2. *Perameles sobbei* sp. nov., paratypes, A, B, RM₂ QMF43879, occlusal view; C, D, LM₄ QMF43880, occlusal view. Scale bars 1mm.

with its lowest point just lingual to its buccal corner.

REMARKS. This species is placed in *Perameles* based on its anterior cingulid being significantly lower than the apex of the paraconid, the result of the low position of the anterior cingulid on the crown (Smith, 1972).

P. allinghamensis is known only from an isolated right M², which is larger than that of all other extant *Perameles*. While *P. sobbei* is known only from lower dentition, it is smaller than extant species such as *P. nasuta* and *P. gunnii*, hence is extremely unlikely to be referable to *P. allinghamensis*.

P. sobbei is clearly distinguished from *P. bougainville*, *P. eremiana*, and *P. bowensis* by its much larger size.

P. sobbei is most similar in size to *P. nasuta* and *P. gunnii*, but differs from those species by possessing the following combination of features: (1) smaller P₂ and P₃, (2) longer M₁, (3) narrower M₃, (4) rounded lingual corner of the anterior cingulid on M₂₋₄, (5) hypoconulid reduced on M₁ and absent from M₂₋₃, and (6) closer approximation of entoconid and hypoconid on M₄.

AFFINITIES. *Perameles sobbei* shares a combination of plesiomorphic and apomorphic

TABLE 1. Measurements of type specimens of *Perameles sobbei* from QML796. All measurements are maximum distances in mm. Length is the anterior-posterior distance. Cent. width is the width across the central cuspids of a premolar. Ant. width is the lingual-buccal distance across the trigonid. Post. width is the lingual-buccal distance across the talonid. Parad = paraconid, metad = metaconid, protod = protoconid, entod = entoconid, hypod = hypoconid.

Tooth	Length	Cent. width	Ant. width	Post. width	metad - parad	metad - protod	Entod hypod
RP ₁	2.92	1.05	N/A	N/A	N/A	N/A	N/A
RP ₂	3.08	1.26	N/A	N/A	N/A	N/A	N/A
RM ₁	4.05	N/A	1.96	2.33	1.09	1.18	1.85
RM ₂	4.03	N/A	2.30	2.46	1.12	1.17	1.70
RM ₃	3.87	N/A	2.11	2.10	0.87	1.10	0.99 (approx.)
LM ₁	3.81	N/A	2.14	1.41	1.04	1.53	indet.

morphological characters with most modern *Perameles* species. Muirhead et al. (1997) suggested that *P. bougainville* is the most plesiomorphic of the recent species by reason of its possession of the following combination of characters: (1) equidistant paraconids, metaconids and protoconids, (2) a more widely separated paraconid and metaconid in comparison to other recent species, and (3) an incomplete anterior cingulid on M₁. The plesiomorphic characters of equidistant trigonid cuspids and relatively widely separated paraconid-metaconid also occur in *P. bowensis* (Muirhead et al., 1997) and in *P. sobbei*.

In common with all recent *Perameles* except *P. eremiana*, *P. sobbei* has a relatively straight cristid obliqua, a condition regarded as plesiomorphic by Muirhead et al. (1997), who noted the autapomorphic trait was a more concave cristid obliqua as part of a narrower talonid. Like *P. eremiana*, a narrower talonid is also present in *P. sobbei*, but alternatively may have arisen by the closer approximation of the entoconid and hypoconid.

Perameles sobbei and *P. bowensis* are the only species of the genus with the synapomorphic reduced hypoconulid on M₃. In all other known species (with the possible exception of *allinghamensis* in which the M₃ is unknown) the hypoconulid is prominent, functioning as an extension of the crown, as well as providing support for the succeeding tooth.

The M₄ attributed to *P. sobbei* possesses a closely approximated entoconid and hypoconid, a trait regarded by Muirhead & Filan (1995) as representing the plesiomorphic condition. This is unlike all recent *Perameles* species, which exhibit the apomorphic condition in which the entoconid is conical in shape and is clearly distinct from the hypoconid. Comparison with the condition in *P. bowensis* is not possible due to

the poor state of preservation of the M₄ talonid in the known material.

P. bowensis is more plesiomorphic than *P. sobbei* in the possession of a pre-entocristid on the M₂. However, on the basis of the synapomorphic condition of the reduction of the hypoconulid on M₁ and its absence from M₃, *Perameles sobbei* is here regarded as the sister taxon to the early Pliocene *P. bowensis*. In other respects, notably in sharing the characters of equidistant trigonid cuspids and wider paraconid-metaconid, both species are more plesiomorphic than *P. nasuta*, *P. gunnii* and *P. eremiana*. The relationship of the *P. sobbei*-*P. bowensis* clade to *P. bougainville* remains unclear, but following Muirhead et al. (1997), the *P. sobbei*-*P. bowensis* clade may represent a sister clade to the *P. nasuta* - *P. gunnii* - *P. eremiana* clade.

Bartholomaj (1977) noted slightly smaller tooth dimensions in the *Perameles nasuta* population from the Pleistocene fissure-fill deposits of Gore, south-eastern Queensland, than those in modern Queensland populations, but did not consider the differences sufficient to warrant specific separation. While the possibility of a similar morphocline relation may also exist between the Pliocene *P. bowensis* and Pleistocene *P. sobbei*, the much greater size difference and slight morphological differences between the two, is here considered sufficient to warrant specific separation.

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LITERATURE CITED

- APLIN, K. P. & ARCHER, M. 1987. Recent advances in marsupial systematics with a new syncretic classification, Pp. xv-lxxii in M. Archer (ed.), *Possums and Opossums: Studies in Evolution*. Surrey, Beatty & Sons and the Royal Zoological Society of New South Wales, Sydney.
- ARCHER, M. 1976. Bluff Downs local fauna, Pp. 383-397. In Archer, M. & Wade, M., *Results of the Ray E. Lemley expeditions, Part 1. The Allingham Formation and a new Pliocene vertebrate fauna from northern Queensland*. *Memoirs of the Queensland Museum* 17: 379-397.
- BARTHOLOMAI, A. 1977. The fossil vertebrate fauna from Pleistocene deposits at Cement Mills, Gore, southeastern Queensland. *Memoirs of the Queensland Museum* 18: 41-51.
- CUVIER, G. L. C. F. D. 1817. *Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*. Volume 1. (Deterville: Paris) 540p.
- FREEDMAN, L. 1967. Skull and tooth variation in the genus *Perameles*. Part I: Anatomical features. *Records of the Australian Museum* 27: 147-166.
- GEOFFROY, E. 1804. *Mémoire sur un nouveau genre de mammifères à bourse, nommé Péramèles*. *Annales de la Musée Natioanl d' Histoire Naturelle de Paris* 4: 56-64.
- GRAY, J.E. 1825. Outline of an attempt at the disposition of the Mammalia into tribes and families with a list of the genera apparently appertaining to each tribe. *Annals of Philosophy* (new series) 10: 337-344.
- GRAY, J.E. 1838. On a new species of *Perameles*. *Proceedings of the Zoological Society of London* 1838: 1.
- KIRSCH, J. A. W. 1968. Prodrum of the comparative serology of Marsupialia. *Nature*, London 217: 418-420.
- LUCKETT, W.P. 1993. An ontogenetic assessment of dental homologies in therian mammals. Pp. 182-204 in Szalay, F.S., Novacek, M.J. & McKenna, M.C. (eds) *Mammal phylogeny, Volume 1*. Springer-Verlag, New York.
- MACKNESS, B.S., WROE, S., MUIRHEAD, J., WILKINSON, C. E. & WILKINSON, D. M. 2000. First fossil bandicoot from the Pliocene Chinchilla Local Fauna. *Australian Mammalogy* 22: 133-136.
- MOLNAR, R.E. & KURZ, C. 1997. The distribution of Pleistocene vertebrates on the eastern Darling Downs, based on the Queensland Museum collections. *Proceedings of the Linnean Society of New South Wales* 117: 107-134.
- MUIRHEAD, J., DAWSON, L. & ARCHER, M. 1997. *Perameles bowensis*, a new species of *Perameles* (Peramelemorphia, Marsupialia) from Pliocene faunas of Bow and Wellington Caves, New South Wales. *Proceedings of the Linnean Society of New South Wales* 117: 163-173.
- MUIRHEAD, J. & FILAN, S. L. 1995. *Yarala burchfieldi*, a plesiomorphic bandicoot (Marsupialia, Peramelemorphia) from Oligo-Miocene deposits of Riversleigh, northwestern Queensland. *Journal of Paleontology* 69: 127-134.
- QUOY, J.R.C. & GAIMARD, J.P. 1824. *Zoologie*: P. 56 in *Voyage autour du Monde*. Freycinet, L. C., de (ed.), Pillet Ainé, Imprimeur-Libraire: Paris.
- OWEN, R. 1877. *Researches on the fossil remains of the extinct mammals of Australia; with a notice of the extinct marsupials of England*. J. Erxleben: London.
- SMITH, M. J. 1972. Small fossil vertebrates from Victoria Cave, Naracoorte, South Australia. II. Peramelidae, Thylacinae and Dasyuridae (Marsupialia). *Transactions of the Royal Society of South Australia* 96: 125-137.
- SPENCER, W. B. 1897. Description of two new species of marsupials from central Australia. *Proceedings of the Royal Society of Victoria* n. s. 9: 5-11.
- SZALAY, F. 1982. A new appraisal of marsupial phylogeny and classification. Pp. 621-640 in M. Archer (ed.), *Carnivorous marsupials*. Surrey Beatty & Sons and Royal Zoological Society of New South Wales, Sydney.

PTERONETA DEELEMEN-REINHOLD AND A REMARKABLE SYMPATRIC
CLUBIONA (CLUBIONIDAE: ARANEOMORPHAE: ARACHNIDA) IN NORTHERN
AUSTRALIA

ROBERT J. RAVEN AND KYLIE S. STUMKAT

Raven, R.J. & K. S. Stumkat 2002 5 31: *Pteroneta* Deeleman-Reinhold and a remarkable sympatric *Clubiona* (Clubionidae: Araneomorphae: Arachnida) in northern Australia. *Memoirs of the Queensland Museum* 48(1): 199-206. Brisbane. ISSN 0079-8835.

Pteroneta spinosa, and similar sympatric *Clubiona pseudopteroneta* are described from north Queensland. The concept of *Pteroneta* and a possible synapomorphy for the Clubionidae are noted. □ *Araneomorphae, Clubionidae, taxonomy, Australia, distribution.*

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Generic diversity of clubionid spiders is greater in northern than southern Australia where *Clubiona* and *Cheiracanthium* dominate. *Clubiona* and *Matidia* Thorell have long been known in north Queensland. Deeleman-Reinhold (2001) transferred *Cheiracanthium* from the Miturgidae back to the Clubionidae and included *Pteroneta* and *Calamoneta*.

Clubionids are commonly encountered in ecological surveys using sweeping, beating and, more rarely, pitfall trapping. Most are nocturnal hunters. Among survey collections from Cape York, males with strong, porrect chelicerae with similar dorsal spination and (in freshly preserved material) blue internal lobes evident through the coxae and carapace cuticle were considered to be a species of *Clubiona*. However, the blue lobes are clearly those of the midgut diverticula and had previously been reported only in *Pteroneta* (Ono, 1989; Deeleman-Reinhold, 2001). Closer determination of tarsal features recognised separate species belonging to *Clubiona* and *Pteroneta*.

Pteroneta Deeleman-Reinhold, 2001 is remarkably *Clubiona*-like but is easily recognised by the setal flag—a brush of long thick hairs along the ventral and prolateral surface of the tarsi (Fig. 3A, C, D)—on tarsi II. Females have also retained the striking blue lobes of the midgut diverticula. The more common of the two previously confused species belongs to widespread *Clubiona* which has many species still undescribed in Australia. This paper was originally intended to describe only the new *Pteroneta* species but its similarity with the sympatric *Clubiona* and compromised generic boundaries necessarily expanded its limits.

SYSTEMATICS

Family CLUBIONIDAE Subfamily CLUBIONINAE

Both species described here have a condition not previously reported in Clubioninae. The setation around the tarsal claws and the size of the claws themselves is different on the front and back pairs of legs. On legs I, II (Fig. 1A) the hairs do not form a tuft, whereas on III, IV a distinct cluster of hairs is evident (Fig. 1B). The claws on I, II are small and concealed by the hairs but on III, IV, although the tuft is distinct so too are the larger claws. We have found the condition present in other *Clubiona* species and contrasting with that in other groups (e.g. Sparassidae, Corinnidae) in which the tufts are similar size on all legs. Should the condition prove to be informatively distributed it may be another synapomorphy of the Clubionidae.

Pteroneta Deeleman-Reinhold, 2001

Pteroneta Deeleman-Reinhold, 2001:145.

TYPE SPECIES (by original designation). *Pteroneta saltans* Deeleman-Reinhold, 2001.

DIAGNOSIS. Differs from all other clubionid genera by the setal flags on tarsus II of ♂♂ and ♀♀ (Fig. 3A, C, D).

DESCRIPTION. Anterior eye row equally spaced. All eyes of similar size. PME much closer to lateral eyes than to each other. Tibia I with 2 pairs of spines ventrally; tibia II, III spineless or with 1-2 spines in line. Leg formula 4213. Setal flags on tarsus II of males and females. Sternum without constriction anteriorly. Male palp typical of *Clubiona* basic form.

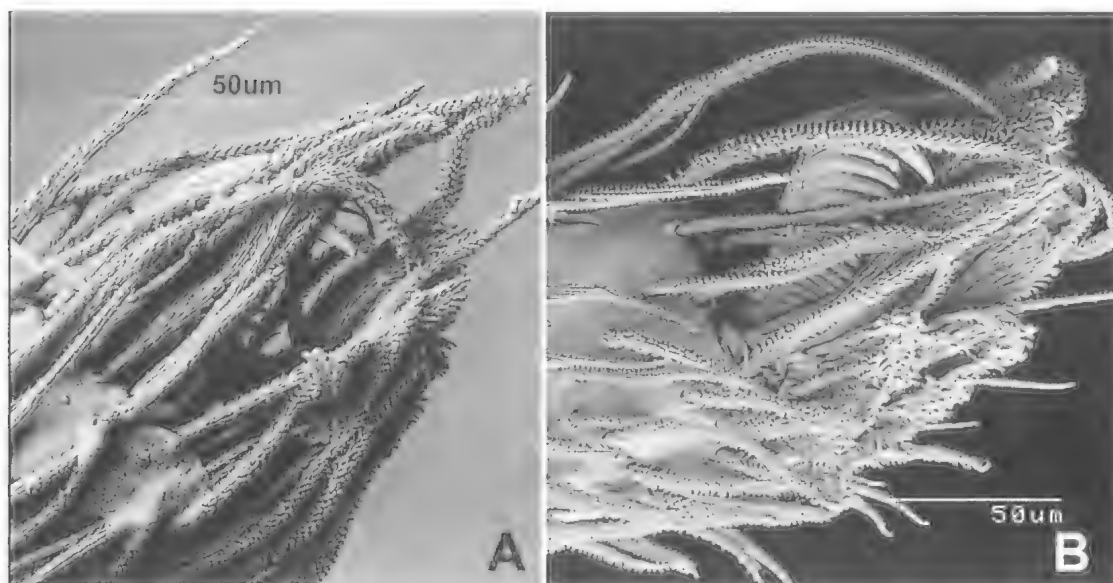


FIG. 1. *Clubiona pseudopteroneta*, sp. nov. SEMs. A, tarsus II, ♂, lateral view showing weak setation and small claw; B, tarsus IV, showing dense tuft and large claw.

SPECIES INCLUDED: *P. saltans* Deeleman-Reinhold, 2001, *P. tertia* Deeleman-Reinhold, 2001, *P. ultramarina* (Ono, 1989), *P. spinosa* sp. nov.

DISTRIBUTION. Southern Japan, Malaysia, Borneo, Sulawesi, Sumba, northern Queensland.

***Pteroneta spinosa* sp. nov.**
(Figs 2, 3, 5E, 6D, E; Tables 1, 2)

MATERIAL. HOLOTYPE: QMS39414, ♂, Lockerbie, Cape York, 10°47'S, 142°27'E, 30 Jan 1975, R.J. Raven. **PARATYPES:** QMS54287, ♂, same data as holotype; QMS31444, ♀ allotype, West Claudie R, Iron Ra, 12°44'S, 143°13'E, 3-10 Dec 1985, G. Monteith, D. Cook; QMS39409, ♀, Mission Beach (S3), 17°55'S, 146°03'E, flight intercept trap, 4 Dec 1995-2 Jan 1996, M. Cermak. All in rainforest in Cape York, Queensland.

DIAGNOSIS. Differs from *P. saltans* Deeleman-Reinhold, 2001 by the dorsal spines on the chelicerae of males, from *P. tertia* Deeleman-Reinhold, 2001 by the more numerous and extensive dorsal spines on the chelicerae, and from both in the dorsal prong off the blade-like tibial apophysis. It differs from *P. ultramarina* (Ono, 1989) by the longer tibial apophysis and relatively longer tegulum in males and females by the larger spermathecae. It differs from *C. pseudopteroneta* sp. nov. in the setal flags on tarsi II.

DESCRIPTION. *Holotype male.* Carapace 1.78 long, 1.28 wide. Abdomen 1.78 long, 0.88 wide. Total length 4.5. Presumably bleached by

prolonged contact with white plastic vial caps. Entirely yellowish fawn; no blue ducts evident.

Carapace. Slightly flattened ovoid in shape, posteriorly convex; eye region smoothly constricted; glabrous. Fovea short, straight, starts at posterior third. Clypeus gradually sloped.

Eyes. 8, all similar in size, pearly in 2 rows; front straight, back slightly procurved. ALE & PLE on common but low tubercle. AME a little further apart than to ALE; PME closest to AME, PME-PME=ca. 2-3 times PME-PLE. MOQ much wider behind than in front by 2 PME widths but about as long as wide in front, PME slightly ovoid, about 5 diameters apart and 2-3 from PLE. Lateral eyes about 1 of their widths apart. Group is width of head.

Chelicerae. Porrect, long with 15-20 short strong conical spines down anterior face in broad band. Base of fang with large triangular tooth on each side, furrow bowed for distal 2/3, large tooth on anterior promargin at distal 1/3 and similar large tooth at retrolaterally proximal of half length of furrow. Fang elongate, longitudinal; basally broad, constricting quickly in distal half.

Maxillae. Elongate with short basal neck; apically with inner bevel forming distinct pointed tip; at widest only ca. 1.4 times width at neck. Labium longer than wide with basal

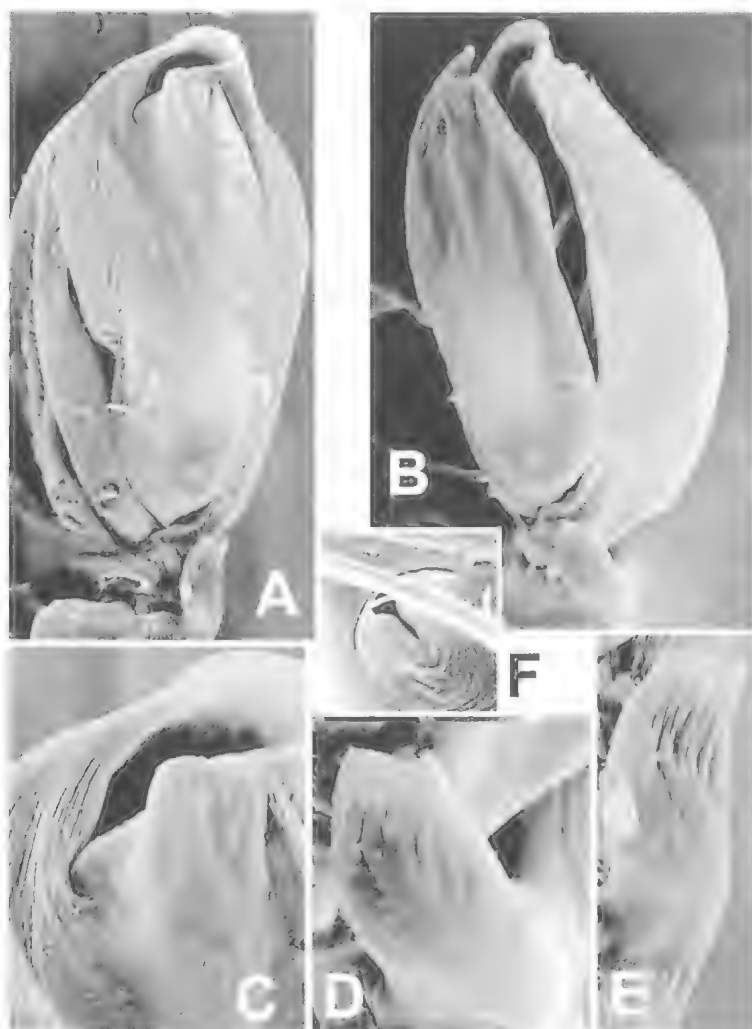


FIG. 2. *Pteroneta spinosa*, sp. nov. SEMs. A-E, ♂ palp. A, B, tibia, bulb and cymbium, ventral view (A) and retrolateral view (B). C, embolus and tegular process. D, tibial apophysis, retrolateral (D) and ventral (E) views. F, tarsal organ.

constriction; separated from sternum by procurved groove.

Sternum. Spearhead-shaped, glabrous, margins hardly sclerotised; posterior corners with intracoxal sclerites.

Legs. 4213. Legs I, II laterigrade. Distinct brush on tarsi II making it appear curved and thick; tarsi II ca. 0.8 length of metatarsi II; hairs of the brush lightly spinulate (Fig. 2D). Metatarsi III with 2 preening combs. Scopula entirely absent. No tibial fracture or tarsal rod.

Claws. Short, hooked, concealed by hairs, 6-9 teeth; claw tufts large, dense bipartite as high as claws on III, IV; weak, nominal tufts on I, II.

Spines. On tibiae and metatarsi I, II, ventral spines weak. I: fe p2d3; pa 0; ti v2.2 (no apical spines); me v2 basal. II: fe pld2; pa 0; ti v1.1; me v1.1. III: fe p2d2; pa 0; ti plv1.1; me pl.1.lrl.1vl + combs. IV: fe dlrl; pa rl; ti plrlvl; me p2r2v1.2. Palp: fe dl.2.

Palp (Fig. 2). Cymbium a typical *Clubiona*-like scoop with ovoid scopulate area dorsoapically; retrobasally with ventral lobe and excavation opposite blade-like acuminate tibial apophysis with secondary dorsal prong. Bulb with large dominant tegulum with low domed apical ridge just concealing cylindrical embolus passing over distal bulb and under retrodistal corner of cymbium; sperm duct passes through oval zone for length of outer tegulum; the sperm duct path is very similar to that in *P. saltans*.

Spinnerets. Set on separated ring from abdomen. ALS are long cones with short apical segment; PMS are cylinders; PLS longer but half diameter of ALS.

ALLOTYPE FEMALE. As for male except:- Carapace 1.48 long, 1.16 wide. Abdomen 2.16 long, 1.16 wide. Total length 4. Blue gut visible in pedicel with flecks through dorsal abdomen, ventral abdomen with lateral 2-3 anastomosing stars per side and median cluster with serial lobes.

Chelicerae. Without strong setae dorsally; not enlarged and with small teeth, 5 on promargin, 3 on retromargin.

Legs. II with much shorter metatarsi + 1/2 length of tarsus incrassate distally down curved with dense twisting flared brush prolaterally. Tarsal organ (Fig. 2F) low, long, keyhole-shaped with wide proximal aperture narrowing quickly.

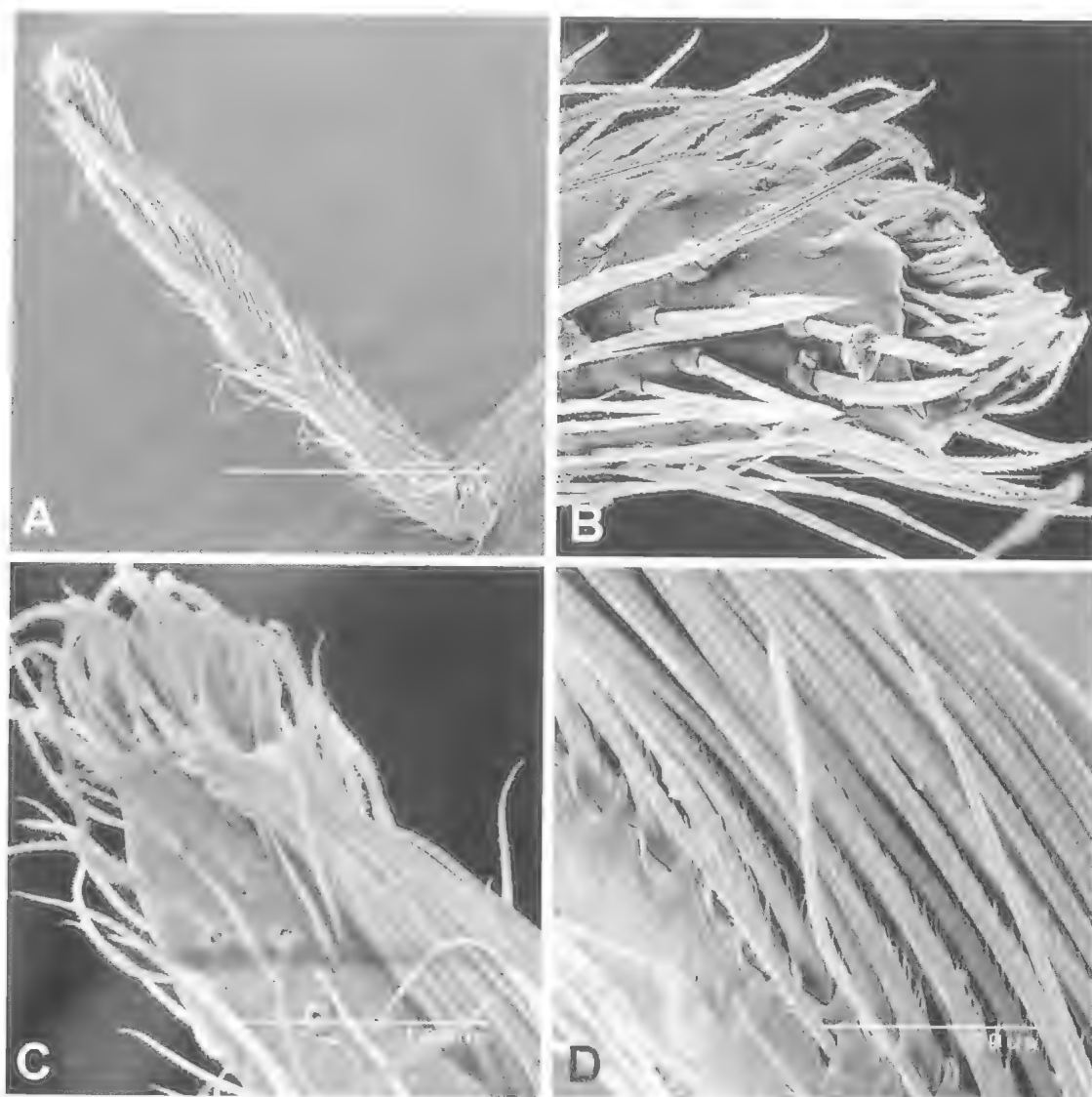


FIG. 3. *Pteroneta spinosa*, sp. nov. SEMs, ♀. A, tibia, metatarsus and tarsus II, prolateral view. B, apex of palpal tarsus, retrolateral view. C, tarsus II, prodorsal view showing trichobothria. D, hairs of special brush on tarsus II, prodorsal view.

Table 1. Leg measurements of *Pteroneta spinosa*, holotype male

	I	II	III	IV	Palp
Femur	1.03	1.25	0.81	1.25	0.47
Patella	0.56	0.59	0.38	0.53	0.22
Tibia	0.94	1.16	0.56	1.06	0.22
Metatarsus	0.66	0.69	0.72	1.16	
Tarsus	0.38	0.53	0.28	0.34	0.44
Total	3.57	4.22	2.75	4.34	1.35

Table 2. Leg measurements of *Pteroneta spinosa*, allotype female

	I	II	III	IV	Palp	
Femur	0.68	0.89	0.71		0.89	0.31
Patella	0.37	0.39	0.29		0.35	0.12
Tibia	0.62	0.83	0.39		0.81	0.17
Metatarsus	0.37	0.35	0.39		0.85	
Tarsus	0.29	0.48	0.29		0.37	0.27
Total	2.33	2.94	2.07		3.27	0.87

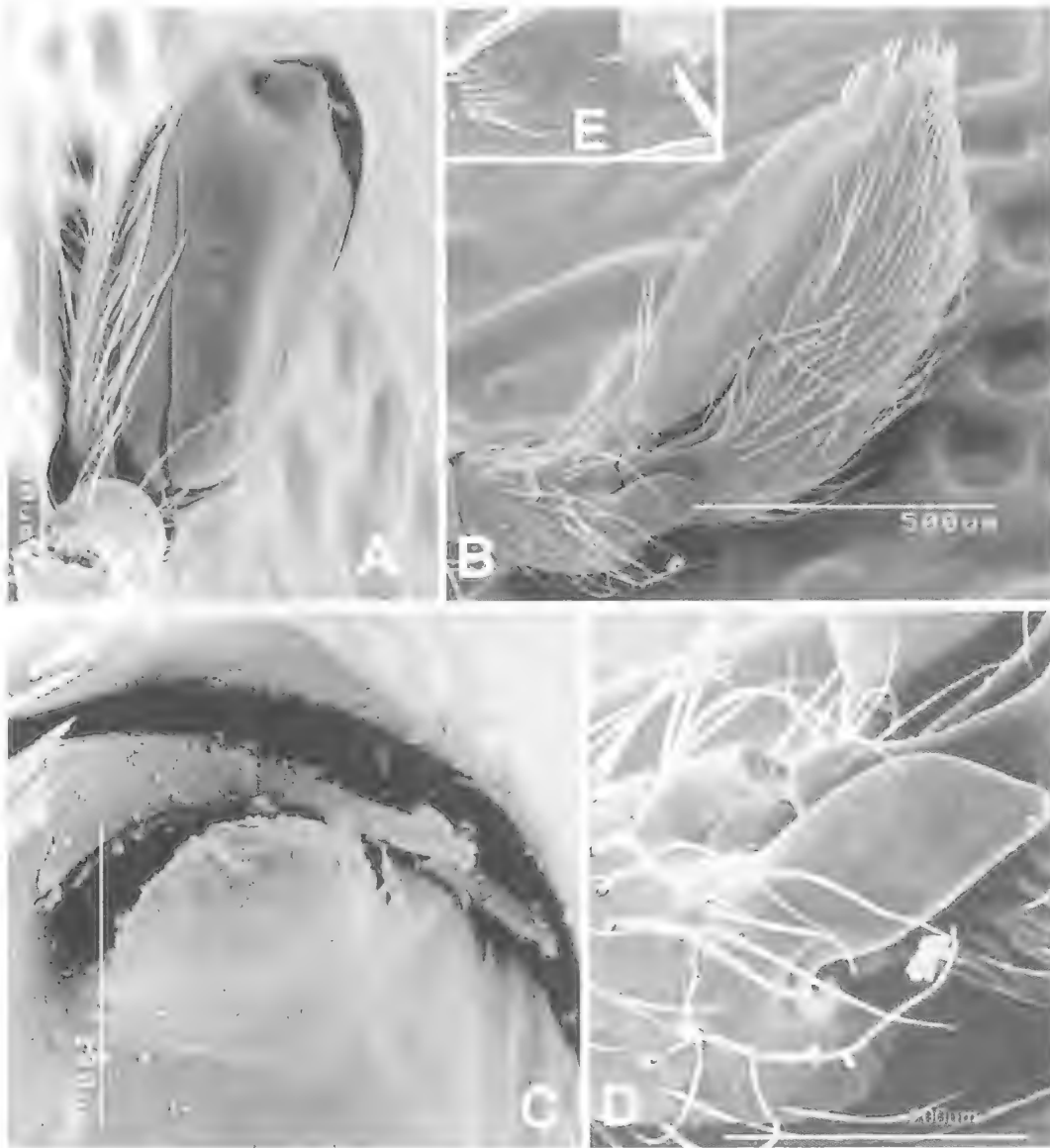


FIG. 4. *Clubiona pseudopteroneta*, sp. nov. SEMs. A-D, ♂ palp. A, B, tibia, bulb and cymbium, ventral view (A) and retrolateral view (B). C, embolus and conductor. D, tibial apophysis and basal cymbium, retrolateral view. E, tarsal organ (left) and trichobothrial base (right).

Trichobothrial bases with 1-4 lateral wings (Fig. 3E, right).

Spines. I: fe d2; pa 0; ti v2.2; me v2. II: fe d2; pa 0; ti 0; me v1.1. III: fe d2; pa 0; ti d1; me p3r2v1.2 + preening comb. IV: fe d2; pa r1; ti r2v1.1; me plr2v1.2.1. Palp: fe d2.

Palp. Tarsus sharply truncate distally with small claw concealed by small claw tufts

Epigyne. Bursae small, ovoid (Fig. 6E), subovate receptacula with ectal lobe and smaller overlying lobe.

DISTRIBUTION & HABITAT. Rainforest between Cairns and Bamaga at the tip of Cape York.

REMARKS. Deeleman-Reinhold (2001:148) listed 2 unidentified females (not examined) from

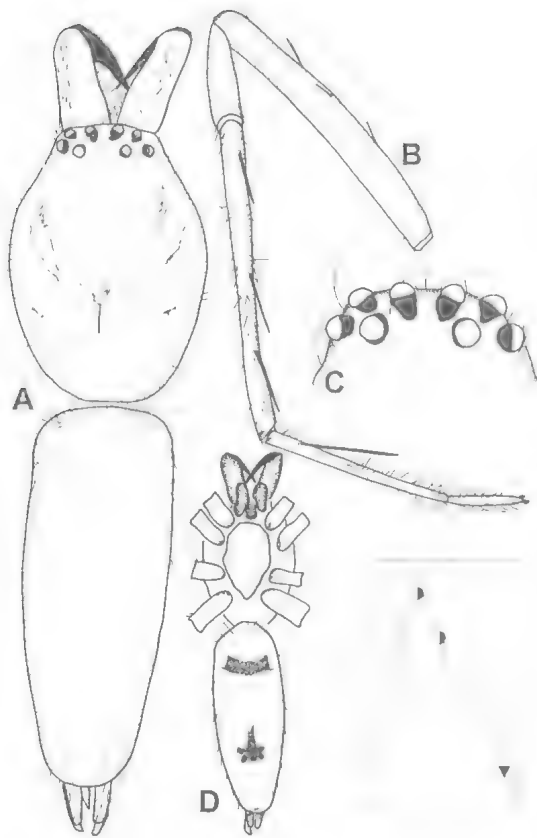


FIG. 5. *Clubiona pseudopteroneta*, sp. nov., holotype, ♂. A, cephalothorax and abdomen, dorsal view. B, leg II, prolateral view. C, eyes, dorsal view. D, sternum and abdomen, ventral view showing pigment posteriorly. E, Cape York showing localities of *Pteroneta spinosa* and *Clubiona pseudopteroneta*; records of both species are indicated by the bicoloured dot and of only *P. spinosa* by the triangle.

Mossman Creek NP, north Queensland, which are considered *P. spinosa*.

P. spinosa may seem very rare in its range. However, our sampling intensity for Cape York is much less than in areas near Cairns. Hence, it is likely that species in Cape York may become extinct long before they are documented.

Clubiona Latreille, 1804

Clubiona pseudopteroneta sp. nov. (Figs 1, 4, 5, 6A-C; Tables 3, 4)

DIAGNOSIS. Differs from *Pteroneta spinosa* in the absence of the setal flags on tarsus II, and from other known species of *Clubiona* in the combination of spines on the dorsal chelicerae of

males, 3 pairs of long spines ventrally on tibiae I, II, the widespread, presumably plesiomorphic, form of the palpal bulb, and the blue midgut evident through the cuticle.

MATERIAL. HOLOTYPE: QMS31443, ♂, West Claudie R, Iron Ra, 12°44'S, 143°13'E, 3-10 Dec 1985, G. Monteith, D. Cook. PARATYPES: QMS31445, QMS39412, QMS39413, ♂♂, ♀, as for holotype. Gordon Ck, Iron Ra, 12°43'S, 143°19'E, Cape York, 24-30 Jun 1976, QM Party: QMS39415, ♂♂♀♀; allotype, QMS54285, ♀, Lockerbie, 10°47'S, 142°27'E, 30 Jan 1975; QMS54286, ♂, R.J. Raven; QMS39411, ♂, same data but 3km E, G. Monteith. All in Cape York rainforest.

DESCRIPTION. *Holotype Male.* Carapace 2.00 long, 1.47 wide. Abdomen 2.97 long, 1.16 wide. Total length 5.9. In alcohol (for 16 years). Carapace fawn, legs and chelicerae lighter; abdomen almost white; from above coxae I- II with light blue area of midgut diverticula, small flecks of blue in carapace opposite coxae and just in front and behind fovea. Ventral abdomen with post-central large blue multilobate mark with short anterior shaft, genital area with wide brown collar, small transverse brown area in front of spinnerets marks tracheal spiracle; all leg joints yellow brown; maxillae light yellow brown.

Carapace. Slightly flattened ovoid in shape, posteriorly convex; eye region smoothly constricted; striae not evident; caput low, slightly arched; almost glabrous, few fine hairs on lateral margins, one long bristle between AME and two behind PLE. Fovea short, straight, starts at posterior third. Clypeus gradually sloped.

Eyes. 8, pearly in 2 rows; front slightly recurved, back slightly procurved. AME directed up and to side; ALE to front and side; PME up and PLE to side. AME slightly the smallest about 1 diameter apart and from slightly larger ALE. Front row on clypeal edge. MOQ wide behind by 2 PME widths but about as long as wide in front. PME slightly ovoid, about 3 diameter apart and 1 from PLE. Lateral eyes almost continuous. Group is width of head. Tapetum canoe-shaped.

Chelicerae. Porrect, long with 7-10 short strong conical spines down anterior face; boss small, if present. Promargin with large triangular tooth adjacent to base of fang and another smaller but still large tooth along furrow, one small tooth basally on retromargin. Fang elongate; basally broad, constricting quickly in distal half.

Maxillae. Elongate with short basal neck; inner concave ridge evident in paratype, distal concavity short diagonal, apically with inner

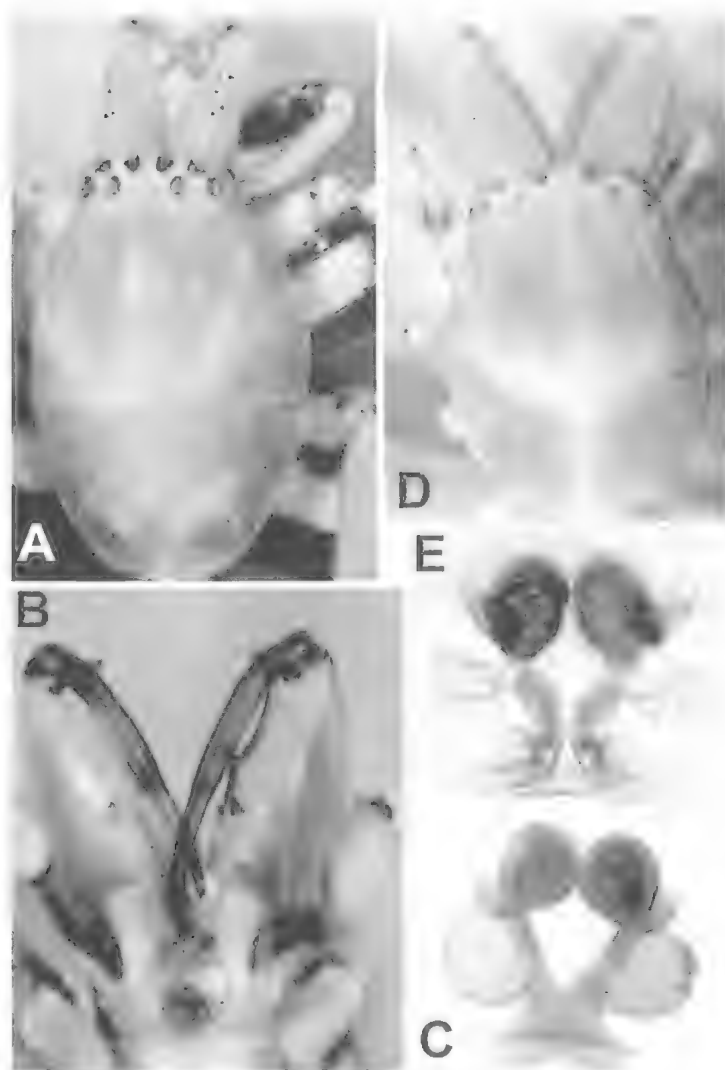


FIG. 6. *Pteroneta spinosa*, sp. nov. (D, E), and *Clubiona pseudopteroneta*, sp. nov. (A-C). A, D, dorsal cephalothorax. B, chelicerae, labium and maxillae. C, E, epigyne.

bevel forming distinct pointed tip. Labium as for *P. spinosa*.

Sternum. As for *P. spinosa*.

Legs. 2413. Inner edges of coxae ventrally gradually curve to sternum, no sharp box-like corners; posterior junction of coxae with sternum a more produced sclerotised lobe than anterior edge; strongest on coxae IV. Legs I-III laterigrade; coxae IV long, making femora IV posteriorly directed over abdomen. Coxae II > I. No brushes on tarsi II or elsewhere. Tarsi short slightly curved; metatarsi ca. 3 times longer;

tibiae longer again. Setation sparse, short erect pallid hairs. Line of 8-10 close hairs pro- and retroventrally distal of spines on tibia I, II. Metatarsi III with 2 preening combs. Scopula entirely absent. No tibial fracture or tarsal rod. Tarsal organ broad, low with longitudinal pectines distally (Fig. 3E).

Claws. Short, hooked with short teeth and small tufts on legs I, II; claws longer with 7-8 long teeth and tufts large, dense bipartite as high as claws on III, IV.

Trichobothria. 2 rows or band on tarsi, 4-5 long, evident on metatarsi, 4-6 long on tibiae.

Spines. Long paired spines on tibia and metatarsi I, II. I: fe p2d3; pa 0; ti v2.2.2; me v2 (very long, unpaired). II: fe p2 d3 pa 0; ti v2.2.2; me v2 (very long, unpaired). III: fe d3; pa 0; ti plv1.1; me pl.1.1r1.1v2.2 + combs. IV: fe d3 v.short; pa r1; ti pl.1r1.1v1.1; me pl.1.1.1.1r1.1.1.1v1.2.1. Palp: fe d1.2; pa d1 (distal). Apical bristle on all patellae.

Palp. Cymbium a "typical" *Clubiona*-like scoop with ovoid scopulate area dorsoapically; retrobasally with ventral lobe and excavation opposite blade-like acuminate tibial apophysis. Bulb flat, large dominant tegulum with low domed apical ridge just concealing cylindrical embolus passing over distal bulb and under retrodistal corner of cymbium; sperm duct as for *Pteroneta spinosa*.

Spinnerets. ALS are long cones with short apical segment; PMS are cylinders; PLS longer but half diameter of ALS. Tracheal spiracle marked by dark brown bar.

ALLOTYPE FEMALE. As for ♂ except:—Carapace 1.75 long, 1.25 wide. Abdomen 2.66 long, 1.41 wide. Total length 4.8.

Chelicerae not correct, without dorsal spines or thick setae; promargin with closely set line of 8 teeth of sizes varying up to 100%; retromargin

TABLE 3. Leg measurements of *Clubiona pseudopteroneta*, holotype ♂.

	I	II	III	IV	Palp
Femur	1.74	2.27	1.34	2.10	0.67
Patella	0.80	0.94	0.54	0.74	0.27
Tibia	1.60	2.30	1.00	1.77	0.34
Metatarsus	1.14	1.50	1.17	2.10	
Tarsus	0.50	0.57	0.40	0.54	0.64
Total	5.78	7.58	4.45	7.25	1.92

with basally converging line of 7 distinctly smaller teeth. Leg formula 4213.

Epigynum. Short predistal transverse ridge with two large basal circular bursae and two closer receptacula distally with ectal lobes.

DISTRIBUTION & HABITAT. Rainforest at Iron Range and Bamaga, Cape York.

REMARKS. Deeleman-Reinhold (2001) splits the *Clubiona* species of SE Asia into a number of species groups. Using her key, this species keys to the *C. hystrix* group. However, it has attributes reported only in *Pteroneta*: spines on dorsal chelicerae, and in *P. tertia* Deeleman-Reinhold, 2001 and *P. ultramarina* (Ono, 1989) and lazulite blue spots visible through the carapace and abdomen. However, tarsi II of ♂ *C. pseudopteroneta* are about 0.25 of length of the metatarsi.

Sexual dimorphism is also evident in relative leg lengths. Most *Clubiona* have a leg formula of 4213. However, although that is true of females of *C. pseudopteroneta* (and most *Clubiona* species described in Deeleman-Reinhold, 2001), it is not true of males (leg formula 2413) and it is not simply a result of measuring regenerated legs. The males of *C. pseudopteroneta* have the second leg longer than the fourth or first.

Most males from Gordon Ck are between 2.00 and 2.60mm in carapace length and are all similar

TABLE 4. Leg measurements of *Clubiona pseudopteroneta*, allotype ♀.

	I	II	III	IV	Palp
Femur	1.06	1.31	0.97	1.50	0.44
Patella	0.50	0.50	0.66	1.25	0.22
Tibia	0.97	1.28	0.66	1.25	0.22
Metatarsus	0.69	0.78	0.72	1.41	
Tarsus	0.34	0.41	0.31	0.47	0.28
Total	3.56	4.28	3.32	5.88	1.16

in chelicerae length dentition and spination dorsally on chelicerae. However, one male has a carapace only 1.62mm long and the chelicerae are hardly correct, each has only 2 spines and small teeth. Also, the carapace of the smallest male is not as long as wide (1.4 vs 1.57) as the other males. The difference in relative carapace shape is expected due to allometric growth but the difference in cheliceral size, spination, and dentition is not expected to be allometric because it is a sexual dimorphism and only 'exists' for the period of the final moult. In any case, care needs to be exercised in the characters noted variable here.

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LITERATURE CITED

- DEELEMEN-REINHOLD, C.L. 2001. Forest spiders of South East Asia. With a revision of the sac and ground spiders (Araneae: Clubionidae, Corinnidae, Liocranidae, Gnaphosidae, Prodidomidae, and Trochanterriidae [sic.]). (Brill: Leiden).
- ONO, H. 1989. New species of the genus *Clubiona* (Araneae, Clubionidae) from Iriomotejima Island, the Ryukyus. Bulletin of the National Science Museum Tokyo (A) 15: 155-166.

THE GREEN TURTLE, *CHELONIA MYDAS*, IN QUEENSLAND: FEEDING ECOLOGY OF IMMATURE TURTLES IN MORETON BAY, SOUTHEASTERN QUEENSLAND

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The diet of immature Green Turtles, *Chelonia mydas*, from the Moreton Banks and Flathead Gutter sites of Moreton Bay, included the available seagrass species and some of the available species of algae. Some animal material was ingested, as were fruits of the Grey Mangrove, *Avicennia marina*. Volumetrically, the seagrass *Halophila ovalis* and the red algae *Gracilaria cylindrica* and *Hypnea spinella* were the most important components of the diet. □ *Green Turtles, Chelonia, feeding ecology, diet, southeastern Queensland, Australia.*

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The Green Turtle, *Chelonia mydas*, is found in most tropical and sub-tropical seas (Groombridge & Luxmoore, 1989). It is the only marine turtle to feed principally on aquatic vegetation (Mortimer, 1982; Bjorndal, 1997), but will also include animal material (Hirth, 1971; Bjorndal, 1997) and mangrove vegetation and fruits in the diet (Pritchard, 1971; Pendoley & Fitzpatrick, 1999; Limpus & Limpus, 2000). Wild populations of Green Turtles feed primarily on seagrass or algae (Bjorndal, 1980; Mortimer, 1982; Bjorndal, 1997). There is, however, ambiguity as to whether *C. mydas* is a selective feeder, ingesting seagrass (or algae) preferentially in an area where both dietary items are available. In a review of the feeding ecology of marine turtles, Mortimer (1982) suggested that Green Turtles consumed algae only when seagrass were unavailable. Bjorndal (1980) reported that immature Green Turtles feeding in the Bahamas rarely consume algae, although it is present in large quantities. Garnett et al. (1985) examined the diet of Green Turtles feeding in Torres Strait, Australia, and could find no evidence to support the theory that turtles feed on algae only when seagrasses were unavailable. Brand (1995) examined the feeding behaviour of juvenile Green Turtles in Flathead Gutter, Moreton Bay and found that individuals were targeting algae, primarily *Gracilaria*.

There is a paucity of detailed analyses on the diet of *C. mydas* in Australian waters. It feeds on algae (Limpus, 1978; Limpus & Reed, 1985a;

Garnett et al., 1985), seagrass (Lanyon et al., 1989), macro-zooplankton (Limpus 1978) and mangrove vegetation and fruits (Read, 1991; Limpus & Limpus, 2000). Forbes (1994) analysed stomach lavage samples from 518 Green Turtles feeding on the reefs surrounding Heron Island, and found that the diet was composed of 38 species of red algae, 21 species of green algae, and 10 species of brown algae. *C. mydas* in this reefal environment were also consuming small amounts of animal material (Forbes, 1994). These data however, are primarily from tropical and algal-based reefal habitats. The present work details the diet of the population of immature Green Turtles feeding in inshore areas of Moreton Bay, southeastern Queensland.

MATERIALS AND METHODS

The turtles of the present study are a subset of those examined for determining the population structure of *C. mydas* in Moreton Bay (Limpus et al., 1994). Turtles were captured in the inter-tidal and adjacent sub-tidal regions of the Moreton Banks (27°20' S, 153°24' E) and Flathead Gutter (27°20'30" S, 153°24'50"E), using the 'turtle rodeo' technique (Limpus, 1978; Limpus & Walter, 1980). Attempts were made to catch all turtles sighted and few evaded capture. Turtles were tagged in the axillary tagging position (Limpus, 1992). The midline curved carapace length (CCL) was measured using a flexible tape (± 0.5 cm) and turtles weighed using a Salter

Spring balance ($\pm 0.5\text{kg}$). The sex and maturity of the majority of Green Turtles were determined via a visual examination of the gonads using laparoscopy (Limpus, 1985; Limpus & Reed, 1985a; Limpus, 1992). Turtles not examined by laparoscopy and whose CCL was less than minimum breeding size for *C. mydas* that breed in eastern Australia ($<90\text{cm}$; Limpus et al., 1984) were assumed to be immature. Turtles were assigned to size classes on CCL: CCL $< 65\text{cm}$ = juvenile (J); CCL $65 < 90\text{cm}$ = sub-adults (SA); CCL $> 90\text{cm}$ and with immature gonads differentiating towards an adult condition = pubescent (P).

Lavage samples were collected from the lower oesophagus (=crop; Thompson, 1980) by stomach flushing (Forbes & Limpus, 1993). Lavage samples of approximately 60-100 grams (wet weight) were usually collected and preserved in 70% ethanol until analysis. Samples were scanned qualitatively to identify contents: seagrasses were identified from keys of Lanyon (1986); algae and Mangrove fruits were identified from keys of Cribb & Cribb (1985). Relative volumes of species in the lavage samples were estimated using principles of stereology (Schaefer, 1970; Gander, 1970). To calculate the percent relative volume of a particular dietary item, the main lavage sample was mixed in a flat-bottomed tray until visually homogeneous. Sufficient sub-sample was randomly removed from the main sample so as to evenly cover the base of a petri dish (85mm diameter). The sub-sample was then analysed under a dissecting microscope at X7, providing a field of view of 15.5mm. Nine fields of the petri dish were examined quantitatively with a graticule that had 36 endpoints of measurement. The first field was selected by placing the petri dish on the microscope stage at a pre-determined co-ordinate; subsequent sites were selected by rotating the petri dish to aligning marks on the side of the petri dish, which sampled the dish without overlap. The relative volumes (%) of the species in the sub-sample were then calculated using formulae (Gander, 1970). Due to the freshness of the lavage samples, most material could be identified to species.

Statistical analyses were performed using the SAS statistics Software Package (1988). The data were initially transformed using an arcsin (\sqrt{P}) correction for proportional data to improve normality and variance homogeneity. Analysis of variance (ANOVA) were performed using the

GLM procedure. Unless otherwise specified, means are ± 1 standard deviation.

STUDY SITE. The Moreton Banks and Flathead Gutter sites, in Moreton Bay, were described in detail by Limpus et al. (1994) and Read (1991). A major geographical feature of the eastern side of Moreton Bay is a large delta comprising the Moreton and Maroom Banks, which are situated between Peel Island, Moreton Island, Crab Island and North Stradbroke Island. These series of shallow sub- and intertidal banks were formed and are maintained by the tidal movement of oceanic and inshore waters through the Rous Channel, the main channel facilitating water flow from the eastern section of Moreton Bay (Milford & Church, 1976). The Moreton Banks ($27^{\circ}24'S$ - $27^{\circ}19'S$) form the northern portion of this delta. Mean air temperatures at Cape Moreton ($27^{\circ}03'S$, $153^{\circ}27'E$) can vary between 26.7°C in January to 13.1°C in July (Bureau of Meteorology, 1999). Surface water temperatures follow the fluctuations of the ambient air temperatures but are generally $2\text{-}3^{\circ}\text{C}$ higher. The Moreton Banks are covered in most areas by 2-6m of water at high tide and varying proportions of the banks are exposed at low tide (Anon, 1987). The Moreton Banks cover $\sim 6290\text{ha}$, with some 2513ha of seagrass meadow and another 3777ha of sparse or patchy seagrass (Hyland et al., 1989). Dominant vegetation of the Moreton Banks includes seagrasses (*Halophila ovalis*, *H. spinulosa*, *Halodule uninervis*, *Zostera capricorni*, *Syringodium isoetifolium*, Hyland et al., 1989) and macro-algae (*Sargassum* sp., *Hypnea spinella*, *Gracilaria cylindrica*, *Hydroclathrus clathratus*, *Codium fragile*). The eastern margin of these banks and Crab Island are fringed by the Grey Mangrove, *Avicennia marina* (Dowling, 1986). A narrow channel that passes between Crab and Moreton Islands, Flathead Gutter, has a sandy substratum, $\sim 3\text{m}$ deep at high tide (Anon, 1987), with a covering of seagrasses and algae on the sloping margins. Seagrass flats bound Flathead Gutter on either side of the channel, with Grey Mangroves growing along their eastern margin.

RESULTS

Between April and October 1991, 199 Green Turtles were captured and sampled for diet from the Moreton Banks and Flathead Gutter, with 31 being recaptured and re-sampled (some more than once), increasing the number of lavage samples to 240. Sex ratio and size classes were

TABLE 1. Sex ratio and size class distribution of immature *Chelonia mydas* sampled from the Moreton Banks and Flathead Gutter sites within Moreton Bay, between April and October 1991.

Sex	Size Class			Total(%)
	Juvenile	Sub-adult	Pubescent	
Female	89	19	1	109(66.5)
Male	39	16	-	55(33.5)
Unknown	27	8	-	35
Total	155(77.9%)	43 (21.6%)	1(0.5%)	199

taken (Table 1). Turtles sampled were predominately from the 10-20kg weight range.

Dietary items identified from lavage samples are listed (Table 2).

Site-specific differences in the mean relative volumes of the common food items ingested were detected. Immature turtles from the Moreton Banks site consumed significantly more *Halophila ovalis* and *Halophila spinulosa* compared to animals from Flathead Gutter, but less *Halodule uninervis*, *Zostera capricorni* and *Gracilaria cylindrica* (Table 3). There were no significant differences between sites for the amount of *Hypnea spinella* consumed.

On the Moreton Banks the seagrass *Halophila*

TABLE 2. Dietary items identified in lavage samples from immature *Chelonia mydas* sampled from the Moreton Banks and Flathead Gutter sites within Moreton Bay, between April and October 1991.

Seagrasses	Family Potamogetonaceae
	<i>Halodule uninervis</i>
	<i>Syringodium isoetifolium</i>
Family Hydrocharitaceae	<i>Zostera capricorni</i>
	<i>Halophila ovalis</i>
	<i>Halophila spinulosa</i>
Algae	Division Rhodophyta
	<i>Hypnea spinella</i>
	<i>Gracilaria cylindrica</i>
	<i>Chondria</i> sp.
	Division Phaeophyta
	<i>Hydroclathrus clathratus</i>
Division Chlorophyta	<i>Cladophoropsis sundanensis</i>
	<i>Caulerpa mexicana</i>
Animal material	Phylum Cnidaria
	Class Scyphozoa
	<i>Catostylus mosaicus</i>
	Class Anthozoa
	<i>Stichodactyla haddoni</i>
	Phylum Arthropoda
Mangrove	Class Crustacea
	<i>Portunus pelagicus</i>
Miscellaneous	Angiospermae
	Verberaceae
	<i>Avicennia marina</i>
	Shell Fragments
	Plant material
	Animal material

Gracilaria cylindrica contributed in excess of 30% in 13.0% and 4% of samples they were identified from. The remaining seagrasses were identified with fairly high frequency but their mean relative volume contribution was usually low (<10%). The cnidarian, *Catostylus mosaicus*, was only identified from nine samples, but its mean relative volume contribution was high (15.4±1.6%). Fruits of the Grey Mangrove were completely absent in the diet of turtles on the Moreton Banks as was the brown alga *Hydroclathrus clathratus*.

TABLE 3. Site-specific dietary differences for immature *Chelonia mydas* from the Moreton Bay region.

Dietary Item	F value	p	Study site mean relative volume ingested (%)	
			Moreton Banks	Flathead Gutter
<i>Halophila ovalis</i>	142.3	0.0001	41.9 ± 0.5	11.4 ± 0.5
<i>Halophila spinulosa</i>	5.6	0.05	5.8 ± 0.4	2.1 ± 0.4
<i>Halodule uninervis</i>	153.1	0.0001	1.1 ± 0.2	6.6 ± 0.2
<i>Zostera capricorni</i>	76.1	0.0001	3.5 ± 0.5	4.3 ± 0.2
<i>Hypnea spinella</i>	0.07	0.08	15.0 ± 0.6	23.0 ± 0.6
<i>Gracilaria cylindrica</i>	76.2	0.0001	11.3 ± 0.7	3.9 ± 0.5

ovalis occurs in the samples with high frequency (92%) and also in the highest mean relative volumes (41.9±0.5%) (Table 4). *Halophila ovalis* contributed mean relative volumes in excess of 30% for 65% of the lavage samples it was identified from. This compares to the red algae, *Hypnea spinella* and *Gracilaria cylindrica*, which occurred in lavage samples with high frequency (63.7% and 31% respectively), but with lower mean relative volumes (15±0.6% and 11.3±0.7%). The red algae, *Hypnea spinella* and

In Flathead Gutter (Table 5), *Halophila ovalis* occurred in samples with lower frequency and in lower mean relative volumes compared to immature Green Turtles feeding on the Moreton Banks, and the algae *Hypnea spinella* and *Gracilaria cylindrica* occurred with high frequencies and high mean relative volumes. The seagrasses *Halodule uninervis* and *Zostera capricorni* were identified with high frequency in lavage samples from this site (96.9% and 90.6% respectively), but contributed little in terms of

TABLE 4. Volumetric analysis of dietary items ingested by immature *Chelonia mydas* from the Moreton Banks site within Moreton Bay, between April and October 1991 (n=113).

Dietary Item	Number of lavage sample with relative volumes				Mean \pm STD	Frequency (%)	Total
	<5%	5<30%	30<50%	>50%			
Seagrasses							
<i>Halophila ovalis</i>	6	33	21	44	41.9 \pm 0.5	92.0	104
<i>Halophila spinulosa</i>	31	12	2	0	5.8 \pm 0.4	39.8	45
<i>Halodule uninervis</i>	44	3	0	0	1.1 \pm 0.2	41.6	47
<i>Zostera capricorni</i>	25	5	0	0	3.5 \pm 0.5	26.5	30
<i>Syringodium isoetifolium</i>	8	3	1	0	7.4 \pm 1.0	10.6	12
Algae							
<i>Hypnea spinella</i>	38	21	4	9	15.0 \pm 0.6	63.7	72
<i>Gracilaria cylindrica</i>	17	14	3	1	11.3 \pm 0.7	31.0	35
<i>Hydroclathrus clathratus</i>	-	-	-	-	-	-	-
<i>Chondria</i> sp.	0	0	0	1	76.0	0.9	1
<i>Cladophoropsis sundanensis</i>	0	1	0	0	7.1	0.9	1
<i>Caulerpa mexicana</i>	3	1	0	0	2.2 \pm 0.9	3.5	4
Mangrove							
<i>Avicennia marina</i>	-	-	-	-	-	-	-
Animal material							
<i>Stichodactyla haddoni</i>	1	2	0	0	6.3 \pm 1.4	2.7	3
<i>Catostylus mosaicus</i>	3	5	0	1	15.4 \pm 1.6	8.0	9
<i>Portunus pelagicus</i>	-	-	-	-	-	-	-
Unidentified animal	11	1	0	0	1.3 \pm 0.4	10.6	12
Miscellaneous							
Unidentified plant	3	0	0	0	1.7 \pm 1.0	2.7	3
Shell fragments	26	3	0	0	1.5 \pm 0.3	25.7	29

mean relative volume (6.6 \pm 0.2% and 4.3 \pm 0.2% respectively). Fruit of *Avicennia marina* were present in 40.2% of lavage samples with a mean relative volume of 8.8 \pm 0.4%.

DISCUSSION

The diet of immature Green Turtles from the Moreton Banks and Flathead Gutter (Tables 4, 5) included algae and seagrasses, fruit of the Grey Mangrove, cnidarians *Catostylus mosaicus* and *Stichodactyla haddoni* and the crustacean *Portunus pelagicus*. Ross (1985) reported that Green Turtles in the northern Indian Ocean ingested seagrasses *Halophila ovalis* and *Halodule uninervis* and most turtles sampled had large quantities of algae in the stomach. Limpus & Reed (1985a) identified Chlorophyta, Phaeophyta and Rhodophyta in last bite samples from *C. mydas* on Heron Reef. Forbes (1994) found that *C. mydas* feeding on reefal habitat around Heron Island were feeding on 38 species of red algae, 21 green algae and 10 brown algae. Based on the stomach contents of 5 *C. mydas* stranded while feeding near the Sir Edward

Pellew Island, NT, the major diet species were *Halodule pinifolia*, with smaller amounts of *Halodule uninervis* and *Halophila ovalis* (Limpus & Reed, 1985b). Species representing the three Divisions of algae and the seagrasses *Cymodocea* sp., *Thalassia hemprichi* and *Halophila spinulosa* were identified in stomach contents from Green Turtles in Torres Strait (Garnett et al., 1985). Lanyon et al. (1989) reported Green Turtles in the shallow bays and estuaries in Australia feed un-selectively on the available species of seagrass. Brand (1995) found that juvenile Green Turtles in Flathead Gutter were feeding on 3 species of seagrass and 3 species of algae. Based on the content of 20 lavage samples, Green Turtles in this site were ingesting some animal material, but fragmentation meant that forage groups could not be identified to species level (Brand, 1995).

Immature Green Turtles were selecting to feed on the seagrasses *Halophila ovalis* and *Halodule uninervis*. These food items have a sparse distribution in the Moreton Banks and Flathead

TABLE 5. Volumetric analysis of dietary items ingested by immature *Chelonia mydas* from the Flathead Gutter site within Moreton Bay, between April and October 1991 (n=127).

Dietary Item	Number of lavage sample with relative volumes				Mean \pm STD	Frequency (%)	Total
	<5%	5<30%	30<50%	>50%			
Seagrasses							
<i>Halophila ovalis</i>	34	23	5	1	11.4 \pm 0.5	49.6	63
<i>Halophila spinulosa</i>	16	2	0	0	2.1 \pm 0.4	14.2	18
<i>Halodule uninervis</i>	57	66	0	0	6.6 \pm 0.2	96.6	123
<i>Zostera capricorni</i>	79	36	0	0	4.3 \pm 0.2	90.6	115
<i>Syringodium isoetifolium</i>	2	0	0	0	1.1 \pm 0.6	1.6	2
Algae							
<i>Hypnea spinella</i>	21	23	11	10	23.0 \pm 0.6	51.2	65
<i>Gracilaria cylindrica</i>	6	33	26	35	39.7 \pm 0.5	78.7	100
<i>Hydroclathrus clathratus</i>	8	0	0	0	1.8 \pm 0.4	6.3	8
<i>Chondria</i> sp.	-	-	-	-	-	-	-
<i>Cladophoropsis sundanensis</i>	1	1	0	0	14.3 \pm 3.1	1.6	2
<i>Caulerpa mexicana</i>	-	-	-	-	-	-	-
Mangrove							
<i>Avicennia marina</i>	23	27	0	1	8.8 \pm 0.4	40.2	51
Animal material							
<i>Stichodactyla haddoni</i>	6	4	0	1	11.7 \pm 1.2	8.7	11
<i>Catostylus mosaicus</i>	2	2	0	0	8.8 \pm 1.6	3.1	4
<i>Portunus pelagicus</i>	1	0	0	0	-	0.8	1
Unidentified animal	22	1	0	0	1.1 \pm 0.2	18.1	23
Miscellaneous							
Unidentified plant	4	0	0	0	1.5 \pm 0.5	3.1	4
Shell fragments	17	0	0	0	0.9 \pm 0.2	13.4	7

Gutter sites (Hyland et al., 1989), and often form seagrass communities with *Zostera capricorni* and *Halophila spinulosa* (Young & Kirkman, 1975). Selective feeding has been reported in previous studies on the feeding ecology of Green Turtles. Bjorndal (1980) reported that immature Green Turtles selected to feed on one species of seagrass, *Thalassia testudinum*, although algae were abundant in the feeding ground. This preference for *T. testudinum* was also noted for immature Green Turtles feeding in Nicaragua (Mortimer, 1981). Mendonca (1983) reported that immature Green Turtles in Mosquito Lagoon, Florida, fed primarily on seagrasses with algae making up a small proportion of the diet, although algae were abundant in the feeding ground. Balazs (1980) suggested that relative abundance and feeding selectivity determined the habits of Hawaiian Green Turtles and Ross (1985) attributed the differential abundance of algal species in the habitat and diet of Green Turtles in Oman to selective feeding. Forbes (1994) also concluded that Green Turtles resident

on Heron Island reef did not ingest algal species based on relative abundance, but fed selectively.

Selection for diet based on algae or seagrass appears to be a feature of distinct populations of Green Turtles or it may be a reflection of insufficient sampling over a limited temporal period. Green Turtles are opportunistic grazers that modify their diet according to composition of the forage. Mortimer (1981) studied the feeding ecology of *C. mydas* from 3 feeding sites in Nicaragua and detected dietary differences attributed to the composition of the local forage and not selectivity. Garnett et al. (1985) studied diets of Green Turtles from 2 sites in Torres Strait, and although there was some selection for soft red algae, no support was found for the hypothesis that turtles fed on algae only when seagrasses were unavailable. Garnett et al. (1985) concluded that the "geographical variation in diets appears to be determined by the relative availability of seagrass and algae and the structure of the local herbivore community." Although some feeding selectivity for seagrasses

Halophila ovalis and *Halodule uninervis* was detected in immature Green Turtles from Moreton Banks, they did not exhibit the selection for a monospecific diet as suggested by Bjorndal (1980). Turtles ingested the seagrasses and algae that were available in the specific feeding area. There is no evidence from this study to support the hypothesis that turtles ingest algae only when seagrasses are unavailable.

Immature *C. mydas* from the Flathead Gutter site were also selecting to feeding on the fruits of the Grey Mangrove. To ingest the fruits of the Grey Mangrove would involve a distinct change from grazing on seagrasses and algae. Green Turtles would either have to forage for fruit floating on the surface or move into the mangle at high tide and feed on the fleshy cotyledons connected to the stem of seedlings or fruit still attached to the tree but covered by water.

There have been few reports of Green Turtles feeding on mangrove vegetation or fruit. Pritchard (1971) recorded Green Turtles in the Galapagos Islands feeding on the foliage and roots of mangroves and Pendoley & Fitzpatrick (1999) recorded Green Turtles in Western Australia feeding on the leaves of the Grey Mangrove. Green Turtles in Shoalwater Bay, an inshore feeding ground on the central Queensland coast, feed on the foliage and fruits of *A. marina*, and rarely on the fruits of *Rhizophora* sp. (Limpus & Limpus, 2000). Vegetation from the mangrove *Rhizophora* sp. has also been recorded from stomach contents of Hawksbill Turtles, *Eretmochelys imbricata* (Bjorndal, 1997). The finding that Green Turtles in Flathead Gutter regularly feed on fruit of the Grey Mangrove poses the question as to whether *C. mydas* may represent a previously unrecognised grazer on mangroves. There are few reports on predators of mangroves. Cattle will freely eat the leaves and fallen seeds of the White Mangrove *Avicennia marina* var. *resinifera* (Everist, 1969). Chapman (1976) reports that large crabs, *Sesarma meinerti* and *S. smithi* are vegetarians, eating fallen leaves and seedlings with the result that they can have a distinct effect upon the rate of regeneration of mangrove forests. There are many sites within Moreton Bay that support large mangrove communities (Dowling, 1986). Many of these are adjacent to deepwater areas and may offer access to this resource for Green Turtles. The level of grazing pressure exerted by *C. mydas* on mangrove vegetation in Moreton Bay remains

unquantified, though the turtles may be having a significant impact on regeneration of seedlings.

The diet of immature Green Turtles in the Moreton Banks and Flathead Gutter were similar to other studies when comparing the amount of animal material ingested. Sixty three (26.3%) of the lavage samples analysed contained some animal material. Garnett et al. (1985) recorded animal material in 52.3% of the 44 stomach contents analysed from *C. mydas* in Torres Strait. Animal material contributed 1.4% of the total dry weight of 243 stomach contents of *C. mydas* from Nicaragua (Mortimer, 1981). Forbes (1994) also recorded animal material from lavage samples taken from 518 Green Turtles at Heron Island. Captive Green Turtles thrive on a diet of fish and crustaceans (Mortimer, 1981) and pelleted food (Wood & Wood, 1981). Green Turtles can digest formulated high protein diets with a high degree of efficiency (Wood & Wood, 1981), and, although it usually constitutes a small proportion of the diet, animal protein may play an important role in the nutrition of this species.

Based on frequency and relative volumes of animal material in lavage samples from immature Green Turtles on the Moreton Banks and Flathead Gutter, we conclude that these turtles are deliberately selecting to feed on these dietary items rather than ingesting them incidentally. To feed selectively on these dietary items involved a distinct change in feeding behaviour that is very different from grazing on seagrasses or algae. To feed on *Catostylus mosaicus*, the turtle must rise into the water column to encounter the cnidarian and turtles have been observed feeding on the cnidarian whilst at the surface (pers. obs., MAR & CJL). The anemone, *Stichodactyla haddoni*, could have been ingested whilst grazing on seagrasses and algae, but it was identified from lavage samples in relative volumes large enough to suggest that it had been deliberately ingested.

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LITERATURE CITED

- ANON. 1987. Wellington Point to the Blue Hole small craft chart. (Queensland Department of Harbours and Marine: Brisbane).
- BALAZS, G. H. 1980. Synopsis of biological data on the green turtle in the Hawaiian Islands. NOAA Technical Memorandum. NOAA-TM-NMFS-SWFC-7.
- BJORNDAAL, K. A. 1980. Nutrition and grazing behaviour of the green turtle, *Chelonia mydas*. Marine Biology 56: 147-154.
- BJORNDAAL, K. A. 1997. Foraging ecology and nutrition of sea turtles. Pp. 199-231. In: Lutz, P. L. & Musick, J. A. (eds) The biology of sea turtles. (CRC Press: Boca Raton) 432p.
- BRAND, S. J. 1995. Diet selection by juvenile green turtles, *Chelonia mydas*, in sub-tropical Flathead Gutter, Moreton Bay. Honours Thesis, Department of Zoology, University of Queensland.
- BUREAU OF METEOROLOGY 1999. Cape Moreton climatic data. Commonwealth Bureau of Meteorology, Canberra.
- CHAPMAN, V. J. 1976. Mangrove vegetation. Cramer.
- CRIBB, A. B. & CRIBB, J. W. 1985. Plant life of the Great Barrier Reef and adjacent shores. (University of Queensland Press: Brisbane).
- DOWLING, R. M. 1986. The mangrove vegetation of Moreton Bay. Department of Primary Industries. Queensland Botany Bulletin 6.
- EVERIST, S. L. 1969. Use of fodder trees and shrubs. Queensland Department of Primary Industries (Div. of Plant Industry) Advisory Leaflet 1024.
- FORBES, G. A. 1994. The diet of the green turtle in an algal-based coral reef community - Heron Island, Australia. Proceedings of the 13th Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum, NMFS-SEFSC 341.
- FORBES, G. A., & LIMPUS, C. J. 1993. A non-lethal method for retrieving stomach contents from sea turtles. Wildlife Research 20: 339-343.
- GANDER, R. 1970. Micro-stereology: practical examples. Microskopion 7: 14-16.
- GARNETT, S. T., PRICE, I. R. & SCOTT, F. J. 1985. The diet of the green turtle, *Chelonia mydas* (L.), in Torres Strait. Australian Wildlife Research 12: 103-112.
- GROOMBRIDGE, B. & LUXMOORE, R. 1989. The green turtle and hawksbill (Reptilia: Cheloniidae): world status, exploitation and trade. CITES, UNEP. 601 p.
- HIRTH, H. F. 1971. Synopsis of biological data on green turtle *Chelonia mydas* (Linnaeus) 1758. FAO Fisheries Synopsis 85.
- HYLAND, S. J., COURTNEY, A. J. & BULTER, C. E. 1989. Distribution of seagrass in the Moreton Region from Coolangatta to Noosa. Queensland Department of Primary Industries Information Series.
- LANYON, J. M. 1986. Seagrasses of the Great Barrier Reef. Great Barrier Reef Marine Park Authority Special Publication 3.
- LANYON, J. M., LIMPUS, C. J. & MARSH, H. 1989. Dugongs and turtles. Grazers in the seagrass system. Pp. 610-634. In Larkum, A. W., McComb, A. J. & Shepherd, S. A. (eds) Biology of seagrasses. A treatise on the biology of seagrasses with special reference to the Australian region (Elsevier: Amsterdam).
- LIMPUS, C. J. 1978. The Reef: An uncertain land of plenty. Pp 187-222. In Lavery, H. (ed.) Exploration north: Australia's wildlife from desert to reef. (Richmond Hill: Richmond, Australia).
- LIMPUS, C. J. 1985. A study of the loggerhead turtle, *Caretta caretta*, in eastern Australia. Ph.D. Thesis, Dept of Zoology, University of Queensland.
- LIMPUS, C. J. 1992. Estimation of tag loss in marine turtle research. Wildlife Research 19: 457-469.
- LIMPUS, C. J. & WALTER, D. G. 1980. The growth of immature green turtles (*Chelonia mydas*) under natural conditions. Herpetologica 36: 162-165.
- LIMPUS, C. J. & REED, P. C. 1985a. The green turtle, *Chelonia mydas*, in Queensland: a preliminary description of the population structure in a coral reef feeding ground. Pp 47-52. In Grigg, G., Shine, R. & Ehmann, H. (eds) Biology of Australian frogs and reptiles. (Surrey Beatty & Sons: Sydney).
- LIMPUS, C. J. & REED, P. C. 1985b. Green sea turtles stranded by Cyclone Kathy on the south-western coast of the Gulf of Carpentaria. Australian Wildlife Research 12: 523-533.
- LIMPUS, C. J. & LIMPUS, D. J. 2000. Mangroves in the diet of *Chelonia mydas* in Queensland, Australia. Marine Turtle Newsletter 89: 13-15.
- LIMPUS, C. J., FLEAY, A. & GUINEA, M. 1984. Sea turtles of the Capricornia Section, Great Barrier Reef. Pp 61-78. In Ward, W. T. & Saenger, P. (eds) The Capricornia Section of the Great Barrier Reef: past, present and future. (Royal Society of Queensland & Australian Coral Reef Society: Brisbane).
- LIMPUS, C. J., COUPER, P. J. & READ, M. A. 1994. The green turtle, *Chelonia mydas*, in Queensland: population structure in a warm temperate feeding area. Memoirs of the Queensland Museum 35: 139-154.
- MENDONCA, M. T. 1983. Movements and feeding ecology of immature green turtles (*Chelonia mydas*) in a Florida Lagoon. Copeia 1983: 1013-1023.
- MILFORD, S. N. & CHURCH, J. A. 1976. Physical Oceanography of Moreton Bay, Queensland. Environmental Physics, Department of Physics, The University of Queensland. Report 1.
- MORTIMER, J. A. 1981. The feeding ecology of the West Caribbean green turtle (*Chelonia mydas*) in Nicaragua. Biotropica 13: 49-58.

- MORTIMER, J. A. 1982. Feeding Ecology of Sea Turtles. Pp. 103-109. In K.A. Bjorndal (ed.) Biology and Conservation of Sea Turtles. (Smithsonian Institution Press: Washington D. C.).
- PENDOLEY, K., & FITZPATRICK, J. 1999. Browsing on mangroves by green turtles in Western Australia. Marine Turtle Newsletter 84: 10.
- PRITCHARD, P.C.H. 1971. Galapagos sea turtles- preliminary findings. Journal of Herpetology 5: 1-9.
- READ, M.A. 1991. Observations on the feeding ecology of immature green turtles, *Chelonia mydas*, in the Moreton Banks region of Moreton Bay, South East Queensland. Honours Thesis, Dept. of Zoology, The University of Queensland.
- ROSS, J.P. 1985. Biology of the green turtle, *Chelonia mydas*, on an Arabian feeding ground. Journal of Herpetology 19: 459-468.
- SCHAEFER, A. 1970. The mathematical basis of stereology. Mikroskopion 7: 3-13.
- THOMPSON, S.M. 1980. A comparative study of the anatomy and histology of the oral cavity and alimentary canal of two sea turtles: the herbivorous green turtle *Chelonia mydas* and the carnivorous loggerhead turtle *Caretta caretta*. M.Sc. Thesis, James Cook University.
- SAS INSTITUTE INC. 1988. SAS/STAT User's Guide, Release 6.03 Edition. Cary, NC. 1028 pp.
- WOOD, J.R., & WOOD, F.E. 1981. Growth and digestibility for the green turtle (*Chelonia mydas*) fed diets containing varying protein levels. Aquaculture 25: 269-274.
- YOUNG, P. C. & KIRKMAN, H. 1975. The seagrass communities of Moreton Bay, Queensland. Aquatic Botany 1: 191-202.

ULTRASTRUCTURE OF THE SPERMATOZOA OF *LITORIA LONGIROSTRIS* (HYLIDAE, ANURA, AMPHIBIA): MODIFICATIONS FOR PENETRATION OF A GELATINOUS LAYER SURROUNDING THE ARBOREAL EGG CLUTCH

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Scheltinga, D.M., Jamieson, B.G.M. & McDonald, K.R. 2002 5 31: Ultrastructure of the spermatozoa of *Litoria longirostris* (Hylidae, Anura, Amphibia): modifications for penetration of a gelatinous layer surrounding the arboreal egg clutch. *Memoirs of the Queensland Museum* 48(1): 215-220. Brisbane, ISSN 0079 8835.

Spermatozoa of *Litoria longirostris* are highly modified for its unique mode of fertilisation and differ distinctively from the sperm of the 10 *Litoria* species previously examined. *L. longirostris* spermatozoa are longer in head, tail and total. The head is long and straight with a distinct acrosome vesicle compared to a short curved head in other *Litoria* spermatozoa. The acrosome vesicle is well developed and surrounds approximately the apical third of the perforatorium only. The perforatorium is a solid homogenous rod that attaches to the nucleus asymmetrically along one side. The nucleus and midpiece are similar in size and structure to those of other *Litoria* species. The axial fibre is greatly enlarged and a juxta-axonemal fibre at doublet 3, usual in anuran sperm, is absent.

Although the spermatozoa of *L. longirostris* are highly modified, having secondarily lost the bufonoid synapomorphy of a putative conical perforatorium consisting of fibres, it can still be distinguished as a ebufonoid by the mitochondrial collar. Thus, we assert that sperm morphology is correlated with phylogenetic relationships as well as mode of fertilisation and that spermatozoal morphology can provide useful information in resolving phylogenetic relationships. □ *Frog, spermatozoa, ultrastructure, fertilisation, Litoria longirostris.*

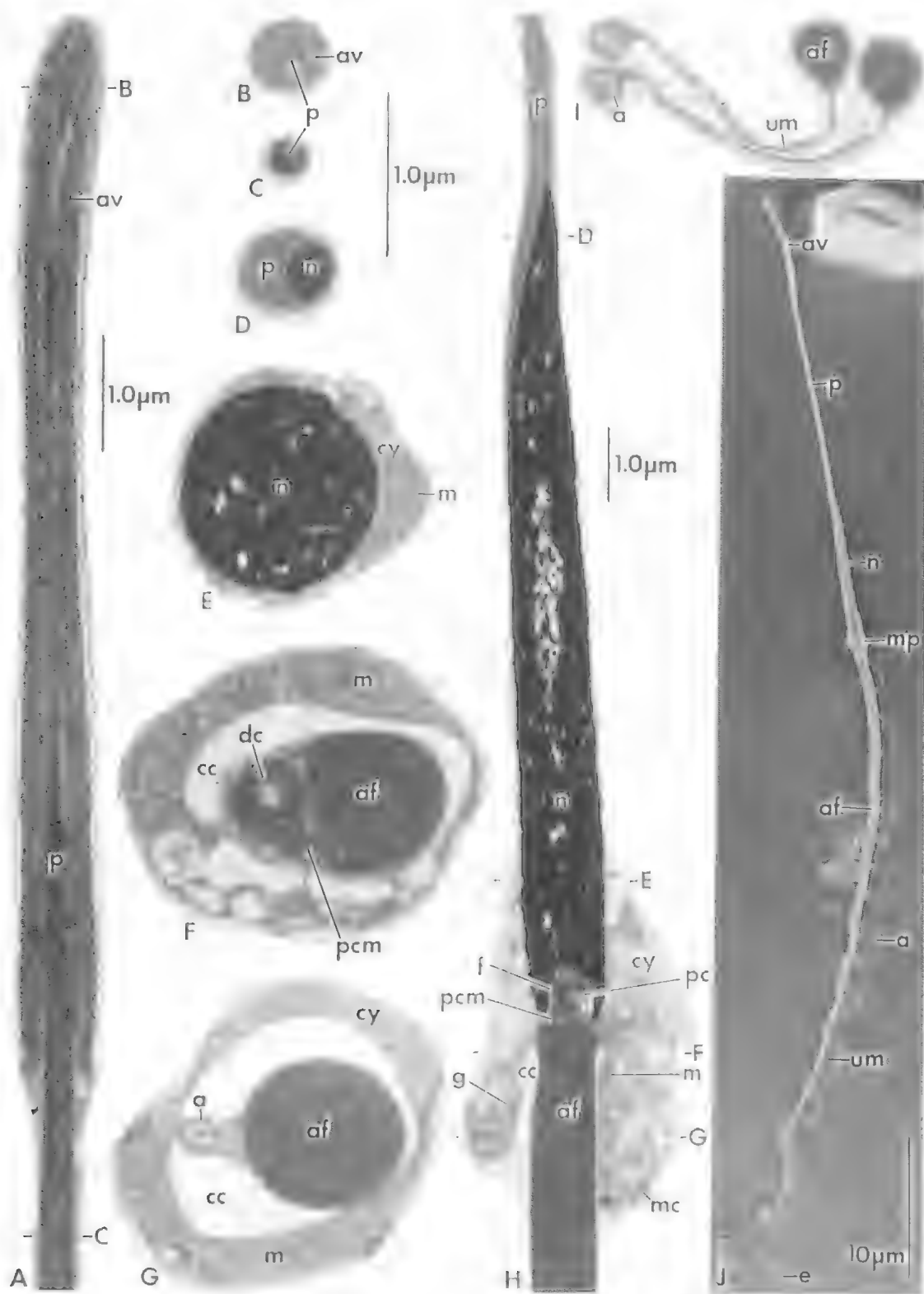
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Litoria longirostris is a relatively small (ca 25mm) grey-brown frog inhabiting the granite upland, rainforest streams of the McIlwraith Range, Cape York Peninsula, Queensland. It is unique amongst Australian frogs in its reproductive mode of depositing egg clutches on vegetation and rocks overhanging water bodies in rainforest streams (McDonald & Storch, 1993). The lime green eggs are large (2.0-2.4mm diameter) and surrounded by a 6mm thick gelatinous capsule. Tadpoles in the clutch are similar in colour to the eggs during development, before turning a pale brown on the dorsal surface prior to hatching. Parental care has been observed with adult frogs straddling the clutch (McDonald & Storch, 1993). The exact method of amplexus and fertilisation remains unknown.

Sperm ultrastructure has previously been examined in 10 species of the Australian hylid *Litoria*: *aurea*, *caerulea*, *eucnemis*, *fallax*, *gracilentia*, *lesueuri*, *moorei*, *peronii*, *rheocola* and *rubella* (Lee & Jamieson, 1993; Meyer et al., 1997; Jamieson, 1999). Although these frogs reproduce in a wide variety of habitats, their

sperm are similar. With regard to correlation of reproductive mode with sperm structure, Garrido et al. (1989) noted that complex flagella occur in species in which fertilisation occurs in a non-aquatic environment and in which development may be viviparous, direct, or aquatic. In terrestrial breeders, notably some of the foam-nesting rhacophorids, the spermatozoon reaches its highest degree of modification. Male *Rhacophorus arboreus*, *R. schlegelii* and *Chiromantis xerampelina*, which shed their sperm onto a foam nest, have highly modified "corkscrew shaped" sperm (Oka, 1980; Mainoya, 1981; Mizuhira et al., 1986; Wilson et al., 1991; Jamieson, 1999). However, in some foam-nesting rhacophorids, as well as those like *Buergeria buergeri* which do not build a foam-nest but lay their eggs in streams, the spermatozoa have a long head and thin tail, neither of which is spiral (Fukuyama et al., 1993; Kuramoto, 1996; Kuramoto & Joshy, 2000, 2001).

The 'arboreal-nesting' reproductive method of *L. longirostris* is similar to that of several species from divergent anuran families (Duellman &



Trueb, 1986) and thus allows correlation between terrestrial nesting and sperm ultrastructure to be further examined. We here give the first description of the spermatozoon of *L. longirostris*.

MATERIALS AND METHODS

Three male *L. longirostris* Tyler & Davies, 1977 were collected from near egg clutches at Upper Peach Creek, McIlwraith Range, North Queensland, on 26-27 September 1995 (QMJ62099, J62100, J62102). The frogs were killed with a lethal injection of sodium pentobarbital shortly after capture. The testes were quickly removed and fixed for transmission electron microscopy (TEM) in 3% glutaraldehyde in 0.1M sodium phosphate buffer (pH 7.2) at 4°C for at least two hours before being transported at ambient temperature to Brisbane for processing and sectioning. On arrival in Brisbane, material for TEM examination was diced into 1mm³ pieces and rinsed in 0.1M sodium phosphate buffer; post-fixed for 80 min in similarly buffered 1% osmium tetroxide; rinsed in buffer; dehydrated through an ascending ethanol series; and infiltrated and embedded in Spurr's epoxy resin (Spurr, 1969).

Sections were cut with a diamond knife on a LKB 2128 UM IV microtome. Thin sections, 50-80nm thick, were collected on carbon stabilised, collodion-coated, 200µm mesh copper grids, stained for 30 s in Reynold's lead citrate (Reynolds, 1963), rinsed in distilled water, then placed in 6% aqueous uranyl acetate for 4 min, rinsed in distilled water, and stained for a further 2 min in lead citrate before final rinsing. Electron micrographs were taken on an Hitachi 300 electron microscope at 75kV and a JEOL 100-s electron microscope at 60kV.

A drop of glutaraldehyde-fixed spermatozoa, for examination by scanning electron

microscopy (SEM), was placed on a clean small round cover slip. Dehydration of the spermatozoa through an ascending ethanol series and final amyl acetate was achieved by adding a drop of each reagent in turn, after removal of the previous fluid with filter paper. The spermatozoa were subjected to critical point drying, gold sputter coated, and photographed on a JEOL 6400 SEM.

Photographs of spermatozoa, from glutaraldehyde-fixed tissue squashes, were made using an Olympus BH2 microscope with Nomarski interference contrast and attached OM-2 camera.

RESULTS

The testicular spermatozoa of *L. longirostris* are filiform and average 82.7µm (n=20, SD=3.3) in length (range 74.1-87.2µm). The spermatozoon is composed of a straight head region (acrosome complex and nucleus) 34.2µm long (n=9, SD=1.9), a midpiece 2.49µm long (n=5, SD=0.32), and a tail 46.3µm long (n=11, SD=1.7) (Fig. 1J). Under light microscopy a distinct acrosome vesicle, perforatorium, nucleus, midpiece, axial fibre, undulating membrane and axoneme can be clearly seen.

ACROSOME COMPLEX. The acrosome complex is 24.6µm long (n=6, SD=1.1) and composed of an elongate cylindrical acrosome vesicles surrounding the apical portion of the putative perforatorium (Fig. 1A,J). The acrosome vesicle is 10.4µm long (n=5, SD=0.08), membrane bound and filled with moderately electron-dense material (Fig. 1A,B). The perforatorium continues posteriorly without any associated structures for some distance before attaching asymmetrically to one side of the nucleus (Fig. 1C,D,H). The perforatorium is a single unit, not divided into separate sheaves/fibres, with a constant diameter throughout its

FIG. 1. *Litoria longirostris*. A-I, TEM. A, Longitudinal section (L.S.) of the apical region of a spermatozoon, showing the acrosome vesicle surrounding only the anterior region of the perforatorium; B-G, Successive transverse sections (T.Ss) through the spermatozoon as indicated; B, through the apical region of the acrosome complex; C, through the perforatorium; D, through the junction of the perforatorium and nucleus; E, through the posterior region of the nucleus; F, through the distal centriole; G, through the midpiece; H, L.S. of the nucleus (showing the perforatorium lying along one side of the nucleus, see also D) and midpiece (showing the mitochondrial collar); I, T.S. of the tail. Note the absence of a juxta-axonemal fibre at doublet 3 and the relatively large axial fibre (see also F and G); J, Whole testicular spermatozoon shown by SEM, showing the head (acrosome vesicle, perforatorium and nucleus), midpiece and tail (axial fibre, undulating membrane and axoneme). B-G and I to the same scale as indicated. A, H and J scales as indicated. Abbreviations: a = axoneme; af = axial fibre, av = acrosome vesicle; cc = cytoplasmic canal; cy = cytoplasm; dc = distal centriole; e = endpiece; f = nuclear fossa; g = putative glycogen granules; m = mitochondrion; mc = mitochondrial collar; mp = midpiece; n = nucleus; p = perforatorium; pc = proximal centriole; pcm = pericentriolar material; um = undulating membrane.

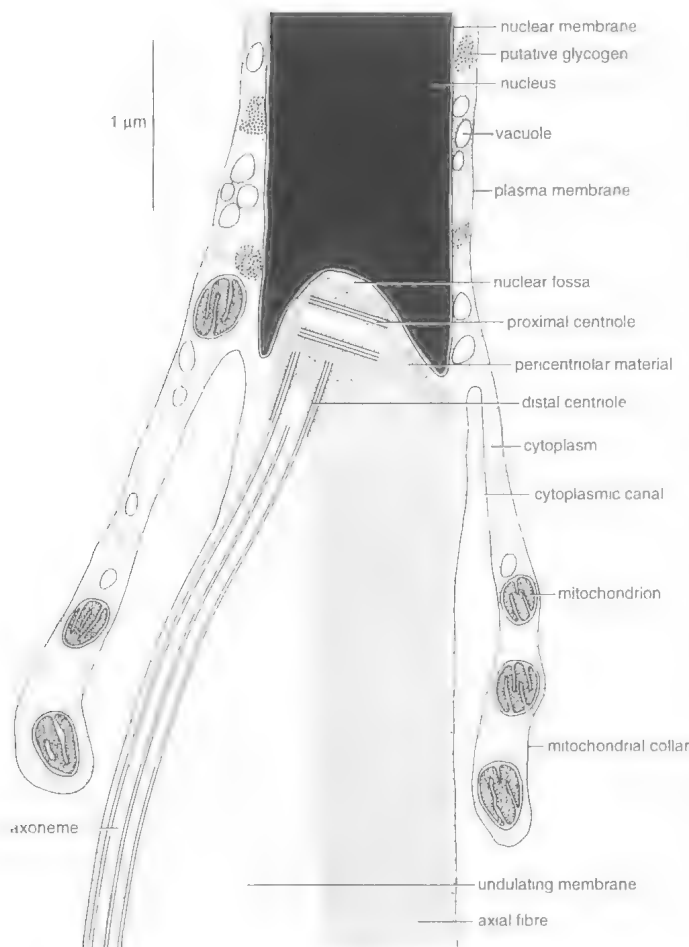


FIG. 2. Drawing of a longitudinal section through the neck region of a spermatozoon of *L. longirostris*. Drawn from a TEM micrograph.

length, is moderately electron-dense and is not bounded by a membrane.

NUCLEUS. The nucleus is $11.07\mu\text{m}$ long ($n=2$, $SD=0.09$), cylindrical, and electron-dense (condensed chromatin) (Fig. 1E,H). Anteriorly, the nucleus tapers to a distinct point alongside the perforatorium (Fig. 1H). Distinct nuclear shoulders are absent. At the base of the nucleus a well-developed nuclear fossa is present (Figs 1H; 2). At this level the nucleus is $1.07\mu\text{m}$ in diameter ($n=8$, $SD=0.05$).

NECK/MIDPIECE. Within the basal nuclear fossa lies the proximal centriole which is surrounded by pericentriolar material that connects it to the nuclear fossa, distal centriole and the axial fibre (Figs 1F,H, 2). The proximal centriole lies at $\sim 75^\circ$ to the long axis of the

nucleus and at right angle to the distal centriole which forms the basal body of the axoneme (Fig. 2). Each centriole is composed of 9, circularly arranged, triplets of short microtubules. The axial fibre extends through the neck region to the level of the base of the nucleus (Figs 1H; 2). A short mitochondrial collar, containing scattered mitochondria, vacuoles and putative glycogen granules, surrounds the anterior portion of the tail but is separated from it by a gap, the cytoplasmic canal (Figs 1F-H, 2).

TAIL COMPLEX. The tail complex (Figs 1I,J, 2) is composed of a 9+2 axoneme and an axial fibre, the fibre being connected by a thin undulating membrane to doublet 3. A juxta-axonemal fibre at 3 is absent. The axial fibre is well-developed and circular in transverse section throughout its length. Anteriorly, it is enlarged, being $\sim 0.95\mu\text{m}$ in diameter (Fig. 1F-I). It continues posteriorly, decreasing in diameter, for almost the entire length of the tail resulting in only a very short portion of the axoneme extending as an endpiece (Fig. 1J).

DISCUSSION

Spermatozoa of all 10 species of *Litoria* which have previously been examined (Lee & Jamieson, 1993; Meyer et al., 1997; Jamieson, 1999) are similar to each other. All closely resemble *Bufo* sperm and exhibit the bufonoid synapomorphy of a conical perforatorium of separate sheaves and the eubufonoid synapomorphy of a long mitochondrial collar separated from the tail by a cytoplasmic canal (Pugin-Rios, 1980; Lee & Kwon, 1992; Lee & Jamieson, 1993; Kwon & Lee, 1995). Spermatozoa of *L. longirostris* differ from these *Litoria* species. However, despite these differences the spermatozoa show characters which are synapomorphic for the eubufonoids.

Spermatozoa of *L. longirostris* are easily distinguished from those of the 10 *Litoria* species previously examined. *Litoria longirostris* spermatozoa are longer, $83\mu\text{m}$, compared with $47\text{--}56\mu\text{m}$ in the 6 *Litoria* species examined by

Lee & Jamieson (1993), and the length of the sperm head is approximately twice the length of 14–18 µm recorded in the latter species. The head is long and straight with a distinct well-developed acrosome vesicle, contrasting with a short curved head in the other investigated *Litoria* spermatozoa. The acrosome complex is highly modified relative to the other species. In the latter, a thin walled conical acrosome vesicle completely caps a putative conical perforatorium of separate sheaves of perforatorial material and the acrosome complex symmetrically caps the tapered point of the nucleus. In *L. longirostris*, the acrosome vesicle differs in surrounding only the apical third, approximately, of the perforatorium. The perforatorium differs in being a solid homogenous cylinder that attaches to the nucleus asymmetrically along one side. Most, if not all, of the increase in length of the head in *L. longirostris* is due to the great length of its acrosome complex. It is deduced that *L. longirostris* spermatozoa have secondarily lost the bufonoid synapomorphy of a conical perforatorium consisting of fibres.

In some foam-nesting rhacophorids the sperm head shows modifications different from those of *L. longirostris* and forms a spiral (Oka, 1980; Mainoya, 1981). It is unknown if there are any ultrastructural modifications to the sperm of those foam-nesting rhacophorids that do not show a spiral head.

In view of the fact that the spermatozoa of the 10 previously examined *Litoria* species have such uniform structure despite differing reproductive modes (lotic vs lentic nesting). It seems likely that the acrosomal modifications observed in *L. longirostris* are an adaptation to penetration of the thick gelatinous mass surrounding the large eggs.

The nucleus and midpiece of *L. longirostris* are similar in size and structure to those *Litoria* species previously examined and show the eubufonoid synapomorphy of a mitochondrial collar separated from the tail by a cytoplasmic canal. The tail of *L. longirostris* spermatozoa differs in its length (46 µm compared to 35–40 µm (Lee & Jamieson, 1993)), having a greatly enlarged axial fibre and in the absence of a juxta-axonemal fibre at doublet 3. All previously examined *Litoria* spermatozoa have a juxta-axonemal fibre at doublet 3. Lee & Jamieson (1993) proposed that the enlargement of the juxta-axonemal fibre observed in *L. fallax*, *L. gracilentia* and *L. lesueuri* was a weak

synapomorphy uniting them. It appears that the presence and size of the juxta-axonemal fibre may provide a useful character in the examination of phylogenetic relationships between species of *Litoria*. Conversely, loss of the juxta-axonemal fibre may not be correlated with phylogenetic relationships and may be an adaptation to the unique fertilisation biology of *L. longirostris*.

The spermatozoa of *L. longirostris* differ greatly from those of foam-nesting rhacophorids that have been examined ultrastructurally in tail, in addition to acrosomal, characters. In these rhacophorids the sperm possess two axonemes which are surrounded by microtubules in a pseudocrystalline matrix. Furthermore, juxta-axonemal fibres, axial fibre and undulating membrane are all absent (Mainoya, 1981; Mizuhira et al., 1986; Wilson et al., 1991; Jamieson, 1999). The loss of a juxta-axonemal fibre, axial fibre and undulating membrane appear each to be a synapomorphy of the Ranoidea, though these states are questionably independent of each other. The only notable similarities, albeit superficial, between the spermatozoa of *L. longirostris* and foam-nesting rhacophorids are the asymmetrical attachment of the acrosome complex to the nucleus and the absence of a juxta-axonemal fibre associated with doublet 3. On present evidence it appears that these similarities are homoplasies.

The Mexican hylid *Pachymedusa dacnicolor* has a similar reproductive mode (Bagnara et al., 1986) to *L. longirostris* and is the only other arboreal-nesting frog to have had its spermatozoa examined ultrastructurally (Rastogi et al., 1988). *P. dacnicolor* spermatozoa are very similar to those of the 10 aquatic-nesting *Litoria* species previously examined and thus differ from *L. longirostris* in its acrosome vesicle which completely caps a conical perforatorium composed of fibres and a juxta-axonemal fibre at doublet 3. There is one similarity between the spermatozoa of these 2 arboreal-nesting hylids that may reflect their shared fertilisation biology and that is the thick axial fibre. In both *P. dacnicolor* and *L. longirostris* the axial fibre is approximately 1 µm in diameter compared to a diameter of approximately 0.2 µm in the other *Litoria* examined. However, within the wider Anura, differences in the sperm tail appear more reflective of phylogeny than fertilisation biology (van der Horst et al., 1995; Meyer et al., 1997).

Although the spermatozoon of *L. longirostris*

is highly modified for its unique fertilisation biology it can still be distinguished as that of a eubufonoid by the mitochondrial collar. Thus, we agree with Garrido et al. (1989) that amphibian sperm morphology is correlated with broad phylogenetic relationships (here at the suprafamilial, eubufonoid level) as well as the mode of fertilisation. Therefore, spermatozoon morphology can provide useful information in resolving phylogenetic relationships at various taxonomic levels despite unique fertilisation biology resulting in highly modified spermatozoa.

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LITERATURE CITED

- BAGNARA, J.T., IELA, L., MORRISETT, F. & RASTOGI, R.K. 1986. Reproduction in the Mexican Leaf Frog (*Pachymedusa dacnicolor*). I. Behavioral and morphological aspects. Occasional Papers of the Museum of Natural History, The University of Kansas, Lawrence, Kansas 121: 1-31.
- DUELLMAN, W.E. & TRUEB, L. 1986. Biology of Amphibians. 670 pp. (McGraw-Hill: New York).
- FUKUYAMA, K., MIYAZAKI, K. & KUSANO, T. 1993. Spermatozoa and breeding systems in Japanese anuran species with special reference to the spiral shape of sperm in foam-nesting rhacophorid species. Abstracts. Second World Congress of Herpetology, Adelaide, South Australia. 29th December 1993-6th January 1994, pp. 92-93.
- GARRIDO, O., PUGIN, E. & JORQUERA, B. 1989. Sperm morphology of *Batrachyla* (Anura: Leptodactylidae). *Amphibia-Reptilia* 10: 141-149.
- JAMIESON, B.G.M. 1999. Spermatozoal phylogeny of the vertebrata. Pp. 303-331. In: Gagnon, C. (ed.), The male gamete: from basic science to clinical applications. (Cache River Press: Vienna, USA).
- KURAMOTO, M. 1996. Generic differentiation of sperm morphology in treefrogs from Japan and Taiwan. *Journal of Herpetology* 30: 437-443.
- KURAMOTO, M. & JOSH, S.H. 2000. Sperm morphology of some Indian frogs as revealed by SEM. *Current Herpetology* 19: 63-70.
2001. Scanning electron microscopic studies on spermatozoa of anurans from Indian and Sri Lanka. *Amphibia-Reptilia* 22: 303-308.
- KWON, A.S. & LEE, Y.H. 1995. Comparative spermatology of anurans with special references to phylogeny. *Mémoires du Muséum national d'Histoire naturelle* 166: 321-332.
- LEE, M.S.Y. & JAMIESON, B.G.M. 1993. The ultrastructure of the spermatozoa of bufonid and hylid frogs (Anura, Amphibia): implications for phylogeny and fertilization biology. *Zoologica Scripta* 22: 309-323.
- LEE, Y.H. & KWON, A. S. 1992. Ultrastructure of spermiogenesis in *Hyla japonica* (Anura, Amphibia). *Acta Zoologica* 73: 49-55.
- MAINOYA, J.R. 1981. Observations on the ultrastructure of spermatids in the testis of *Chiromantis xerampelina* (Anura: Rhacophoridae). *African Journal of Ecology* 19: 365-368.
- MCDONALD, K.R. & STORCH, D. 1993. A new reproductive mode for an Australian hylid frog. *Memoirs of the Queensland Museum* 34: 200.
- MEYER E., JAMIESON B.G.M. & SCHELTINGA D.M. 1997. Sperm ultrastructure of six Australian hylid frogs from two genera (*Litoria* and *Cyclorana*): phylogenetic implications. *Journal of Submicroscopic Cytology and Pathology* 29: 443-451.
- MIZUHIRA, V., FUTAESAKU, Y., ONO, M., UENO, M., YOKOFUJITA, J. & OKA, T. 1986. The fine structure of the spermatozoa of two species of *Rhacophorus* (*arboreus*, *schlegelii*). I. Phase-contrast microscope, scanning electron microscope, and cytochemical observations of the head piece. *Journal of Ultrastructure and Molecular Structure Research* 96: 41-53.
- OKA, T. 1980. Ultrastructural observations on the sperm in a frog, *Rhacophorus schlegelii*. *Japanese Journal of Herpetology* 8: 137.
- PUGIN-RIOS, E. 1980. Étude Comparative sur la Structure du Spermatozoïde des Amphibiens Anoures. Comportement des Gamètes lors de la Fécondation. (Unpubl. PhD Thesis, L'Université de Rennes).
- RASTOGI, R.K., BAGNARA, J.T., IELA, L. & KRASOVICH, M.A. 1988. Reproduction in the Mexican Leaf Frog, *Pachymedusa dacnicolor*. IV. Spermatogenesis: a light and ultrasonic study. *Journal of Morphology* 197: 277-302.
- REYNOLDS, E.S. 1963. The use of lead citrate at high pH as an electron opaque stain in electron microscopy. *Journal of Cell Biology* 17: 208-212.
- SPURR, A.R. 1969. A low viscosity epoxy-resin embedding medium for electron microscopy. *Journal of Ultrastructure Research* 26: 31-43.
- VAN DER HORST, G., WILSON, B.A. & CHAN-NING, A. 1995. Amphibian sperm: phylogeny and fertilization environment. *Mémoires du Muséum national d'Histoire naturelle* 166: 333-342.
- WILSON, B.A., VAN DER HORST, G. & CHAN-NING, A. 1991. Scanning electron microscopy of the unique sperm of *Chiromantis xerampelina* (Amphibia: Anura). *Electron Microscopy Society of Southern Africa* 21: 255-256.

NEW RECORDS OF THE WATER MITE *ARRENURUS* FROM AUSTRALIA, WITH
DESCRIPTION OF THREE NEW SPECIES AND ONE NEW SUBSPECIES (ACARI:
HYDRACHNIDIA: ARRENURIDAE)

HARRY SMIT

Smit, H. 2002 5 31: New records of the water mite *Arrenurus* from Australia, with the description of three new species and one new subspecies (Acari: Hydrachnidia: Arrenuridae). *Memoirs of the Queensland Museum* 48(1): 221-232. Brisbane. ISSN 0079-8835.

From northern Australia are described *Arrenurus kimberleyensis*, *A. yorkensis*, *A. recticaudatus* and *A. rostratus mutilus*. Descriptions are provided for a number of females not described before, or described erroneously. *Arrenurus degeneratus*, described as a subspecies of *A. rostratus*, has been raised to a full species. *A. liberatus* Walter and *A. pulcher* Walter are reported new for Australia. Range extensions within Australia are given for a number of species. □ *Hydrachnidia, water mites, Arrenurus, Australia, new species.*

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Of the cosmopolitan water mite genus *Arrenurus* 41 species have been reported from Australia (Harvey, 1998; Smit, 1999). Material dealt with herein come from northern Western Australia and northern Queensland. A number of unidentified females and species not previously reported from Australia in the Viets collection (Senckenberg Museum, Frankfurt a/Main, Germany) have been examined. Most are from northern Australia, a small part comes from New South Wales. In this paper three new species and one new subspecies are described. Descriptions are provided for a number of females not described before, or described erroneously. Finally, two species are reported new for Australia, and a number of range extensions are given for species already known from Australia. The subgenus *Brevicaudaturus* will be treated in a separate paper.

MATERIAL AND METHODS

Unless stated otherwise, all material has been collected by the author. All non-type material has been deposited in the Zoological Museum of the University of Amsterdam.

The following abbreviations are used: A1 and A2 pre- and post-antennal glandularia, Cx2-4 coxoglandularia 2-4, D1-4 dorsoglandularia 1-4; L1-4 lateroglandularia 1-4; V2 ventroglandularia 2; PI-PV palp segments 1-5; IV-leg-4-6 fourth-sixth segments of fourth leg; WAM Western Australian Museum, Perth; QM Queensland Museum, Brisbane; ZMAN Zoological Museum of the University of Amsterdam, Amsterdam,

SMF Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main. For the description of the glandularia Jin & Wiles (1996) and Wiles (1997) are followed. All measurements are in µm, measurements of leg and palp segments are of the dorsal margins. Measurements of paratypes in the description of new species are given in brackets.

SYSTEMATICS

Arrenurus (Arrenurus) acutipetiolatus
Smit, 1999

Arrenurus (Arrenurus) acutipetiolatus Smit, 1999: 225.

MATERIAL. *New South Wales*. ♂, Farmersdam near Gloucester, 19 March 1976, coll. B.V. Timms (slide SMF6196). ♀, pond at Redhead via Newcastle, 12 October 1979, coll. B.V. Timms (slide SMF7376).

REMARKS. Kurt Viets erroneously identified this material as *A. spinifer* Walter or a subspecies of it. However, the shape of the dorsal shield and cauda of *A. spinifer* differs significantly from *A. acutipetiolatus*.

DISTRIBUTION. TAS, VIC and NSW.

Arrenurus (Arrenurus) balladoniensis
Halik, 1940

Arrenurus balladoniensis Halik, 1940: 283.

Arrenurus quadripapillatus Lundblad, 1941: 120.

Arrenurus (Arrenurus) balladoniensis Halik: Halik, 1941: 113; Lundblad, 1947: 74; Cook, 1986: 305; Smit, 1992: 106, 1997: 233; Harvey, 1998: 144.

MATERIAL. *Western Australia*. 1 ♀, Taylor's Lagoon, east of Broome, 14 October 1998. 6 ♂, 13 ♀, Lake Eda, east of Broome. 30 October 1998.

DISTRIBUTION. WA, NT, QLD and VIC.

***Arrenurus (Arrenurus) bifurcatus* Smit, 1999**

Arrenurus (Arrenurus) bifurcatus Smit, 1999: 229.

Arrenurus (Arrenurus) mantonensis Smit (err., non George, 1903); Smit, 1997: 239; Harvey, 1998.

MATERIAL. *Western Australia.* 4 ♀, pool downstream of Manning Gorge, at campground, the Kimberley, 12 September 1998. 4 ♀, Jackeroo's Waterhole, El Questro Station, the Kimberley, 15 September 1998. 2 ♀, Lake Kununurra, 10 km SE of Kununurra, 19 September 1998. ♂, 5 ♀, Spillway Creek near Lake Argyle, 20 September 1998. 6 ♀, Arthur Creek, at crossing with Great Northern Highway, the Kimberley, 23 September 1998.

DESCRIPTION. Some additional measurements and characters are: Males. Body 863-899 long, 641-676 wide, yellowish brown. Females. Body 761-887 long, 705-786 wide. Dorsal shield 664-721 long and 502-551 wide.

DISTRIBUTION. NT and WA.

***Arrenurus (Arrenurus) kimberleyensis* sp. nov.**
(Fig. 1)

ETYMOLOGY. From the Kimberley.

MATERIAL. **HOLOTYPE.** ♂, pools upstream of Bell Gorge Falls, the Kimberley, Western Australia, 11 September 1998 (WAMT42590). **PARATYPES.** 2 ♂, ♀ (WAMT42591), 3 ♂, ♀ (ZMAN type ACAR.0001.1-4.), same data as holotype. ♀, pool Lennard River, east side Windjana Gorge, Windjana Gorge National Park, the Kimberley, 10 September 1998 (ZMAN type ACAR.0002.5.). 2 ♂, ♀, Jackeroo's Waterhole, El Questro Station, the Kimberley, 15 September 1998 (WAM T42592). ♂, 2 ♀ (ZMAN type ACAR.0003.6-8.), Lily Creek Lagoon, Kununurra, 17 September 1998. ♂ (T42593, WAM), Lake Kununurra, 10 km SE of Kununurra, 19 September 1998.

OTHER MATERIAL. *Western Australia.* ♂ (not sclerotised), ♀, Bell Creek at crossing with Gibb River Road, the Kimberley, 10 September 1998. *Queensland.* ♂ (not sclerotised), Tinaroo Falls Dam at Yungaburra, Qld, 16 September 2000.

DIAGNOSIS. Petiole with a rounded basal piece, on which an arrow-shaped part is inserted; dorsal shield tapering posteriorly. Female with elongate dorsal shield; dorsum with moderate sized humps.

DESCRIPTION. Male. Body 1393 (1073-1393) long and 1126 (1021-1126) wide, green, with concave anterior margin. Dorsal shield 526 (478-535) wide, tapering posteriorly, dorsal furrow incomplete; D1 on large humps (Fig. 1A, C). Cauda well-developed, distinctly set off from anterior body part. Pygal lobes well-developed.

Hyaline membrane large, medially pointed (only visible when posterior body part slightly lifted). Petiole consisting of a rounded basal piece, on which dorsally an arrow-shaped part is inserted, which is posteriorly indented. In aberrant male from pools upstream of Bell Gorge Falls, the arrow-shaped part is lacking, and the petiole appears rounded in dorsal view. Genital plates directed perpendicularly to lateral body margin, posterior and anterior margin slightly undulating (Fig. 1B). Lengths of PI-PV: 50, 96, 90, 108, 64. PII with three setae in anteroventral corner (Fig. 1D). Lengths of I-leg-4-6: 219, 203, 259. Lengths of IV-leg-4-6: 336, 198, 243; IV-leg-4 with a spur.

Female. Body 1307 (1552-1618) long, 1146 (1286-1387) wide, with concave anterior margin, truncated posteriorly, with slightly concave posterior margin. Dorsal furrow complete, dorsal shield elongate, 778 (971-993) long, 502 (567-616) wide. D1 and L4 on moderate sized humps (Fig. 1E). Capitular bay V-shaped. Medial margin of fourth coxal plates larger than medial margin of third coxal plates. Medial distance of fourth coxal plates slightly smaller than one genital valve. Gonopore with small, hardly visible chitinised patches. Genital plates large, directed almost perpendicularly to lateral body margin (Fig. 1F); occasionally (young ♀?) lateral part of genital plate slightly enlarged. Lengths PI-PV: 34, 98, 92, 106, 58; palp as in male. Lengths of I-leg-4-6: 211, 186, 198. Lengths of IV-leg-4-6: 227, 243, 227.

REMARKS. The male is distinguished within *Arrenurus* by the shape of its petiole and dorsal shield. The female is close to *A. ensifer* and *A. liliaceus*, the latter species is larger with larger humps (especially L4), a pear-shaped dorsal shield and the posterior body margin is more concave. Differences from *A. ensifer* are not clear, as only one female of this species is known. *A. ensifer* is very similar in body shape, including humps, but has more slender, slightly bowed genital plates. A female from Arthur Creek might belong to the new species, but it is larger (1688 long, 1447 wide), and has larger, slightly bowed genital plates.

Arrenurus (Arrenurus) liberatus
Walter, 1929

Arrenurus (Arrenurus) liberatus Walter: 1929b: 263; Daday, 1898a: 97; Daday, 1898b: 106; K. Viets, 1935: 11; K.O. Viets, 1959: 423; Cook, 1967: 225; Lundblad, 1969: 425; Prasad, 1974: 26; Jin & Wiles, 1996: 333; Jin, 1997: 142; Gledhill & Wiles, 1997: 537.

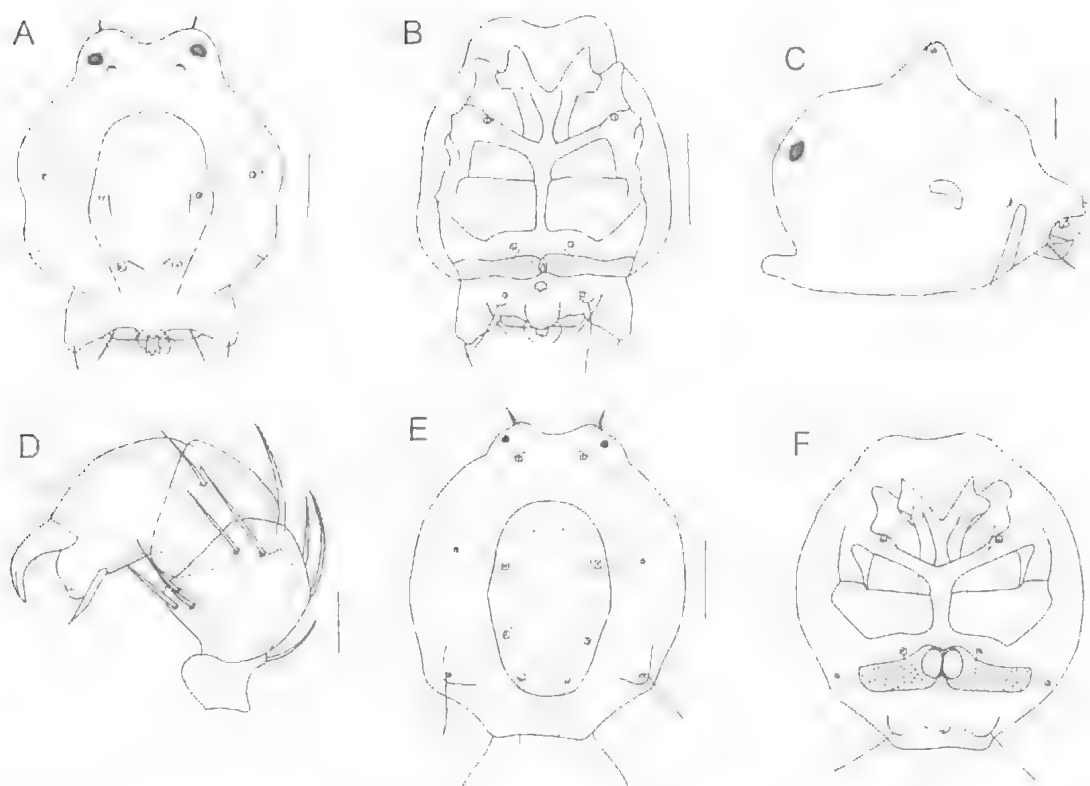


FIG. 1. *Arrenurus kimberleyensis* sp. nov. A-D, holotype ♂; A, dorsal view; B, ventral view; C, lateral view; D, palp. E, F, paratype ♀; E, dorsal view; F, ventral view. Scale bars: A, B, E, F = 400 µm; C = 200 µm; D = 50 µm.

Arrenurus orientalis (part., ♂, err., non Daday, 1898): Daday, 1898a: 97; Daday, 1898b: 107, Piersig & Lohmann, 1901: 92.

MATERIAL. *Queensland*, 1 ♂, Low Lake, Lakeland NP, 5 September 2000.

DISTRIBUTION. China, Burma, Singapore, Sri Lanka, Brunei and Indonesia. It is reported here for the first time for Australia.

***Arrenurus (Arrenurus) liliaceus* Smit, 1997**
(Fig. 2)

Arrenurus (Arrenurus) liliaceus Smit, 1997, 239; Harvey, 1998: 144.

MATERIAL. *Western Australia*, 19 ♂, 19 ♀, Jackeroo's Waterhole, El Questro Station, the Kimberley, 15 September 1998. ♀, Lily Creek Lagoon, Kununurra, 17 September 1998. 12 ♂♂, 3 ♀, Lake Kununurra, 10 km SE of Kununurra, 19 September 1998. 3 ♀, Fitzroy River, S of Fitzroy Crossing, 28 September 1998.

DESCRIPTION. Some additional measurements and characters are:

Male. Body 1467-1779 long, 1065-1206 wide.

Female. Body 1789 (1608-1950) long, 1568 (1427-1598) wide, greenish, occasionally brown, with concave anterior margin. Dorsal furrow complete. Dorsal shield 1045 long, 850 wide, pear-shaped. D1 on large humps, L4 on very large humps (Fig. 2A). Body truncated posteriorly. Medial distance of fourth coxal plates very small. Medial margin of fourth coxal plates much larger than medial distance of third coxal plates. Gonopore 178 long, without chitinous patches. Genital field long, directed more or less perpendicularly to lateral body margin, with an undulating posterior margin (Fig. 2B). Lengths of PI-PV: 51, 128, 98, 150, 98; palp as in male. Lengths of I-leg-4-6: 243, 227, 227. Lengths of IV-leg-4-6: 308, 292, 247.

REMARKS. With more material available, it is clear that the female described by me (Smit, 1997) does not belong to this species, but to an unknown species. The female of *A. liliaceus* is very similar to females of the subgenus *Brevicaudaturus*. However, subgeneric classification

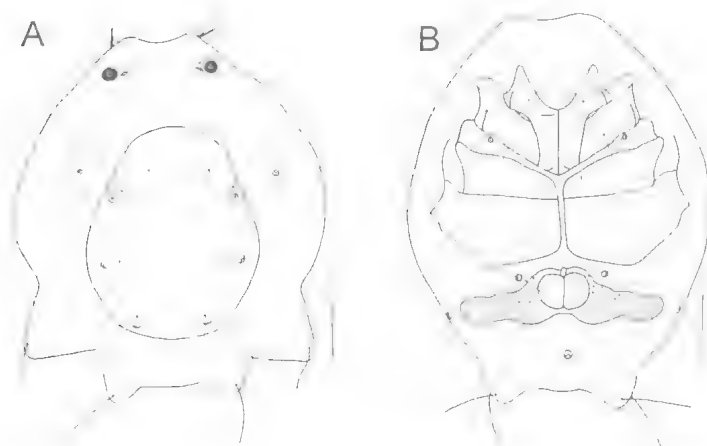


FIG. 2. *Arrenurus liliaceus* Smit, ♀: A, dorsal view; B, ventral view. Scale bars = 400µm.

is based on characters of the males. In young females all the humps are still lacking.

DISTRIBUTION. WA.

***Arrenurus (Arrenurus) yorkensis* sp. nov.**
(Fig. 3)

ETYMOLOGY. From Cape York Peninsula.

MATERIAL. HOLOTYPE. ♂, White Lily Lagoon, Lakefield NP, Qld, 4 September 2000 (QMS 55056). PARATYPES. ♂, 4 ♀ (QMS55057), 2 ♂, 4 ♀ (ZMAN type ACAR.0002.1-6.), same data as holotype; ♂, 10 ♀ (ZMAN type ACAR.0002.7-17.), 10 ♀, (QMS55058), Red Lily Lagoon, Lakefield NP, 4 September 2000; ♂, 8 ♀, shallow pool along road to Hanush Waterhole, Lakefield NP, 4 September 2000 (QMS55059).

DESCRIPTION. Male. Body 818 (794-858) long (including petiole), 516 (527-559) wide, greenish-bluish, with straight to slightly concave anterior border. Dorsal shield 332 (340-360) wide, only D4 on small humps; dorsal furrow passing onto sides of body near pygal lobes. Cauda and pygal lobes short (Fig. 3A). Gonopore 40 long. Genital plates large, widened laterally, swollen and visible in dorsal view (Fig. 3B). Near posterior margin of body a key-shaped structure. Hyaline membrane of two lobe-shaped parts. Petiole open dorsally, anterior half chitinised, posterior half more hyaline. In lateral view, hyaline part downturned, and chitinised part upturned (Fig. 3C). Posterior margin of hyaline part indented. On chitinised part, two setae, best seen in lateral view. Lengths of PI-PV: 26, 60, 48, 60, 34. Medial side of PII with two setae near anterior margin (Fig. 3D). Lengths of I-leg-4-6:

114, 112, 130. Lengths of IV-leg-4-6: 206, 84, 98; IV-leg-4 with a very short spur.

Female. Body 737 (680-810) long, 672 (640-717) wide, broad egg-shaped, posterolateral corners absent. Dorsal shield 470 (454-506) wide, dorsal furrow incomplete. Capitular bay wide, U-shaped. Medial distance of fourth coxal plates smaller than width of one genital valve. Medial margin of fourth coxal plates larger than medial margin of third coxal plates. Posterior margin of fourth coxal plates straight, directed slightly oblique or perpendicularly to lateral body margin. Gonopore large, 154 long; genital valves with small, indistinct chitinised parts

near central part of gonopore. Genital plates relatively short, about two times as long as wide, narrowed laterally (Fig. 3E). Lengths of PI-PV: 26, 58, 50, 64, 32; palp as in male. Lengths of I-leg-4-6: 106, 102, 110. Lengths of IV-leg-4-6: 140, 134, 112.

REMARKS. The new species belongs to a group which occurs mainly in Asia, e.g. *A. ansatus* Walter, *A. kantakaphorus* Cook, *A. dadayi* Cook and *A. cavipetiolatus* Lundblad. All have a long, complicated petiole.

Arrenurus (Micruracarus) anbangbang
Smit, 1997

Arrenurus (Micruracarus) anbangbang Smit, 1997: 246; Harvey, 1998: 144.

MATERIAL. *Arrenurus (Micruracarus) jabiruensis* Smit [part., ♀]. PARATYPES. 4 ♀♀, Lake Jabiru, Northern Territory, 20 July 1994.

OTHER MATERIAL. *Western Australia.* ♀, pool Lennard River, east side Windjana Gorge, Windjana Gorge National Park, the Kimberley, 10 September 1998. ♀, pools upstream of Bell Gorge Falls, the Kimberley, 11 September 1998. ♂, 3 ♀, pools Silent Grove (behind ranger station), the Kimberley, 11 September 1998. 10 ♂, 3 ♀, pool near Adcock Gorge, the Kimberley, 12 September 1998. 16 ♂, 17 ♀, Jack's Waterhole, along Gibb River Road, the Kimberley, 14 September 1998. ♀, pool Amalia Gorge, El Questro Station, the Kimberley, 16 September 1998. ♀, Spillway Creek near Lake Argyle, 20 September 1998. 3 ♂, 4 ♀, Arthur Creek, at crossing with Great Northern Highway, 23 September 1998. ♀, Fitzroy River, S of Fitzroy Crossing, 28 September 1998. *Northern Territory.* ♂, Magela Creek floodplain, Winnamurra Billabong, 23 July 1979, coll. R. Tait (slide SMF 7192).

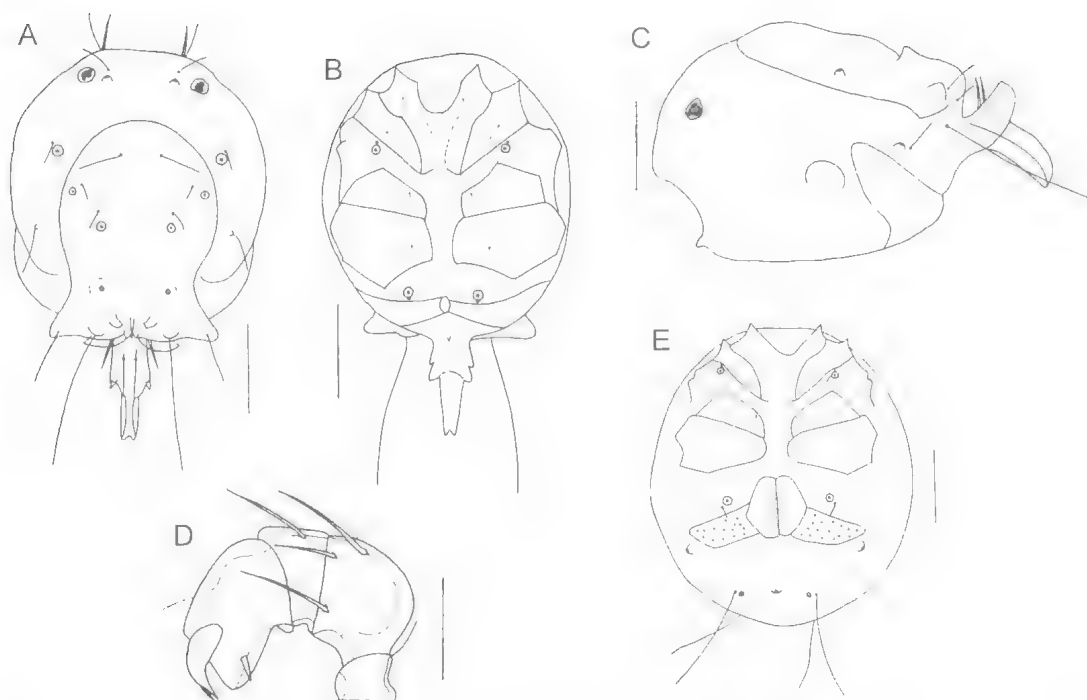


FIG. 3. *Arrenurus yorkensis* sp. nov., holotype ♂: A, dorsal view; B, ventral view; C, lateral view; D, palp. E, *Arrenurus yorkensis* sp. nov., paratype ♀. Scale bars: A,B,C,E = 200µm; D = 50µm.

Queensland. ♂, Lake Emma, Lakefield NP, 3 September 2000. 4 ♂, 5 ♀, Low Lake, Lakefield NP, 5 September 2000. ♂, 3 ♀, swamp 9km E of Musgrave, along road to Lakefield NP, 5 September 2000. ♂, ♀, billabong W of Wenlock River, near crossing with road to Iron RangeNP, 10 September 2000.

REMARKS. Female body shape is variable, many specimens have a more truncated posterior body part compared to specimens in the original description (Smit, 1997). A closer examination of females of *A. jabiruensis* revealed that their palp is similar to that of *A. anbangbang*. Separation of females of *A. anbangbang* and *A. jabiruensis* was based on these two characters. Therefore, females found with males of *A. jabiruensis* must be assigned to *A. anbangbang*.

DISTRIBUTION. NT, WA and QLD.

Arrenurus (Micruracarus) jabiruensis

Smit, 1997

(Fig. 4)

Arrenurus (Micruracarus) jabiruensis Smit, 1997: 249;
Harvey, 1998: 144.

MATERIAL. Northern Territory. ♀, Magela Creek floodplain, Jabiluka Billabong, 19 January 1979, coll. R. Tait (slide SMF7123). 3 ♀, Magela Creek floodplain,

Leichhardt Billabong, 14 May 1979, coll. R. Tait (slides SMF7106, 7107). ♂, ♀, Magela Creek floodplain, Jabiluka Billabong, 16 July 1979, coll. R. Tait (slide SMF7124). ♂, ♀, Magela Creek floodplain, Ja Ja Billabong, 28 September 1979, coll. R. Tait (slides SMF7179, 7181). 2 ♂, 4 ♀, Magela Creek floodplain, Jabiluka Billabong, 1 October 1979, coll. R. Tait (slides SMF7132, 7133, 7137, 7138, 7139). ♀, Magela Creek floodplain, Nankeen Billabong, 4 October 1979, coll. R. Tait (slide SMF7120). 2 ♀, Magela Creek floodplain, Leichhardt Billabong, 19 November 1979, coll. R. Tait (slide SMF7112).

DESCRIPTION. Female. Body 778 (761-810) long, 660 (648-672) wide, bluish, with slightly concave anterior body margin, posteriorly truncated. Dorsal furrow complete, dorsal shield 607 (591-648) long and 486 (486-510) wide. Medial margins of third and fourth coxal plates more or less of equal length. Medial distance of fourth coxal plates slightly less than width of one genital valve. Gonopore 146 long, genital valves with two pairs of rounded chitinous patches. Genital plates twice as long as wide, directing perpendicularly to lateral body margin (Fig. 4). However, genital plates of variable shape, specimens with a more bowed genital plate have been found. Lengths of PI-PV: 27, 60, 40, 74, 36;

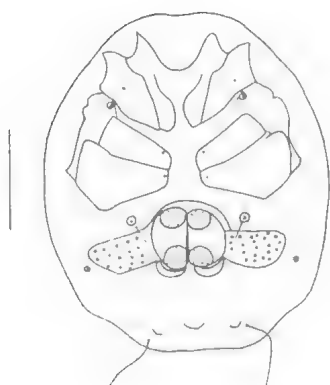


FIG. 4. *Arrenurus jabiruensis* Smit, ♀, dorsal view. Scale bar = 200µm.

PII with three setae on medial side, near anterior margin. Lengths of I-leg-4-6: 108, 122, 100. Lengths of IV-leg-4-6: 156, 150, 132.

REMARKS. Females previously assigned to *A. jabiruensis* are now assigned to *A. anbangbang*. In Viets' collection a number of females found with males of *A. jabiruensis* are here assumed to be females of the species.

The petiole of males consists of a fused ventral and dorsal piece, which sometimes have been loosened as a result of mounting, giving the petiole a quite different appearance. The ventral piece of the petiole has a straight posterior margin, the dorsal piece a slightly concave posterior margin.

DISTRIBUTION. NT.

***Arrenurus (Micruracarus) madaraszi*
Daday, 1898**

Arrenurus madaraszi Daday, 1898a: 97, 1898b: 99; Piersig & Lohmann, 1901: 116; Walter, 1929b: 265; Uchida & Miyazaki, 1935: 73; Miyazaki, 1935: 725, 1936a: 1, 1936b: 306; Uchida, 1937: 26; Imamura, 1953a: 259, 1953b: 275; 1953c: 470, 1954: 164, 1956: 25; Mendis & Fernando, 1962: 98; Fernando, 1963: 34; Lundblad, 1969: 402; Prasad, 1974: 26; Fernando, 1990: 271.

Arrenurus (Micruracarus) madaraszi Daday: Viets, 1935: 20; Uchida & Imamura, 1951: 350; Viets, 1959: 423; Imamura, 1961: 57; Jin & Wiles, 1996: 333; Jin, 1997: 146; Cook, 1967: 223; K.O. Viets, 1973: 108; Reisen & Mullen, 1978: 770; Gledhill & Wiles, 1997: 537; Smit, 1999: 233.

Arrenurus geei Marshall, 1921: 172.

Arrenurus kraepelini Koenike, 1906: 132; Viets, 1926: 100. *Arrenurus palembangensis* Piersig, 1906: 369; Walter, 1923: 197, 1928: 106; Marshall, 1928: 604; Walter, 1929a: 263. *Arrenurus procursus* Viets, 1927: 320; Viets, 1929: 397.

MATERIAL. *Queensland*. ♂, 3 ♀, White Lily Lagoon, Lakefield NP, 4 September 2000. 2 ♂, 5 ♀, shallow pool along road to Hanush Waterhole, Lakefield NP, 4

September 2000. ♂, ♀, Low Lake, Lakefield NP 5 September 2000. ♀, swamp 9km E of Musgrave, along road to Lakefield NP, 5 September 2000. 2 ♂, 2 ♀, Tinaroo Falls Dam at Yungaburra, 16 September 2000.

REMARKS. Both males and females are close to *A. anbangbang*. Its hyaline petiole is for the most part lying free, while the petiole of *A. madaraszi* is fused with the cauda. Moreover, the petiole of *A. madaraszi* has a small knob in the central part. Females are similarly close to each other, but *A. anbangbang* has a truncated posterior body part, and D1 lies on a small tubercle, which is absent in *A. madaraszi*.

DISTRIBUTION. China, Japan, Malaysia, Burma, Singapore, India, Pakistan, Sri Lanka, Indonesia and QLD.

***Arrenurus (Micruracarus) pulcher*
Walter, 1911**

Arrenurus pulcher Walter, 1911: 214; Lundblad, 1969: 405. *Arrenurus (Micruracarus) pulcher* Walter: Viets, 1959: 424. *Arrenurus (Micruracarus) micropetiolatus* (err., non Walter, 1928); Cook, 1967: 223.

MATERIAL. *Queensland*. ♂, 2 ♀, swamp Chili Beach, Iron Range NP 7 September 2000.

REMARKS. Cook (1967) suspected *A. pulcher* and *A. micropetiolatus* Walter to be conspecific. Lundblad (1969) on the contrary, disagreed with this, and assigned Cook's specimen of *A. micropetiolatus* from India to *A. pulcher*.

DISTRIBUTION. Aru Islands (Indonesia), Singapore, India, Burma and QLD.

***Arrenurus (Micruracarus) purpureus*
Smit, 1997**

Arrenurus (Micruracarus) purpureus Smit, 1997: 251; Harvey, 1998: 144.

MATERIAL. *Western Australia*. 4 ♀, Cockatoo Creek, at crossing with Great Northern Highway, 8 September 1998. 1 ♂, 2 ♀, Bell Creek at crossing with Gibb River Road, the Kimberley, 10 September 1998. ♂, 2 ♀, pools upstream of Bell Gorge Falls, the Kimberley, 11 September 1998. ♂, 11 ♀, Jack's Waterhole (along Gibb River Road), the Kimberley, 14 September 1998. 4 ♀, Jackaroo's Waterhole, El Questro Station, the Kimberley, 15 September 1998. ♀, pool Valentine Springs, W of Kununurra, 18 September 1998. 7 ♂, 9 ♀, Spillway Creek near Lake Argyle, 20 September 1998. 3 ♂, pools in creek at Old Halls Creek, S of Halls Creek, 26 September 1998. 2 ♂, Fitzroy River, S of Fitzroy Crossing, 28 September 1998. ♂, Taylor's Lagoon, east of Broome, 14 October 1998.

REMARKS. In contrast to the type material (which were all purple), the body of specimens from this study is green or bluish green.

DISTRIBUTION. WA.

Arrenurus (Micruracarus) queenslandicus
Smit, 1999

Arrenurus (Micruracarus) queenslandicus Smit, 1999: 231.

MATERIAL. PARATYPES. 3 ♂, 5 ♀, pond north of Normanton, 14 August 1989 (ZMAN).

OTHER MATERIAL. *Queensland*. 3 ♂, Red Lily Lagoon, Lakefield NP, 4 September 2000. ♂, pool along road to Hanush Waterhole, Lakefield NP, 4 September 2000. ♂, ♀, Hasties Swamp, Hasties Swamp NP, 6 August 1989; same location, 6 ♂, 8 ♀, 16 September 2000. ♂, Tinaroo Falls Dam at Yungaburra, 16 September 2000.

REMARKS. Smit (1999) mentioned as differences between *A. anhangbang* and *A. queenslandicus* the petiole, which should be fused with the cauda in *queenslandicus*, and be free in *anhangbang*. However, this is not correct, as in the latter species the hyaline petiole is also fused. *A. anhangbang* has a cauda consisting of two broad lobes, while in *queenslandicus* these lobes are narrower. Other characters which separate males of *anhangbang* are D1 on small humps, and a large rounded anteroventral corner of PIV. In males of Hasties Swamp (only in 2000) and Tinaroo Falls Dam, the hyaline petiole is only partly fused with the cauda.

DISTRIBUTION. Queensland.

Arrenurus (Micruracarus) recticaudatus sp. nov.
(Fig. 5)

ETYMOLOGY. For the rectangular male cauda.

MATERIAL. HOLOTYPE. ♂, Spillway Creek, near Lake Argyle, WA, 20 September 1998 (WAMT42594). PARATYPES. 3 ♂, 5 ♀, same data as holotype (WAMT42595). 2 ♀, Jack's Waterhole (along Gibb River Road), the Kimberley, WA, 14 September 1998 (ZMAN type ACAR.0003.1-2.). 2 ♂, 2 ♀, Lake Emma, Lakefield NP, Qld, 3 September 2000 (ZMAN type ACAR.0003.3-7.). OTHER MATERIAL. ♀, Stock Dam, Anakie, Qld, 18 July 1974, coll. B.V. Timms (slide SMF5654). ♀, Lake Kununurra, 10km SE of Kununurra, 19 September 1998.

DIAGNOSIS. Male with a rectangular cauda, posteriorly with a closed cleft, cauda simple. Female with long, widened genital plates and D1, L4 and V2 on humps.

DESCRIPTION. Male. Body 859 (855-859) long, 721 (656-672) wide, brownish green, with concave anterior margin. Dorsal shield complete, rounded, 462 (425-446) long and 397 (365-393) wide. D1 on large humps, D3 on small tubercles. Petiole simple, almost completely fused with cauda, bluntly pointed posteriorly (Fig. 5C).

Cauda more or less rectangular, posteriorly with a closed cleft (Fig. 5A). Medial margin of third coxal plates larger than medial margin of fourth coxal plates. Cx 4 on rounded humps, V4 on large pointed humps, which extend beyond posterior body margin. Genital plates extending to lateral body margin, but acetabula hardly visible (Fig. 5B). Lengths of PI-PV: 36, 66, 46, 70, 50; PII with 2-3 setae on medial side (Fig. 5D). Lengths of I-leg-4-6: 160, 174, 202. Lengths of IV-leg-4-6: 200, 168, 188; IV-leg-4 with a short spur.

Female. Body 887 (859-972) long and 798 (737-810) wide. Anterior body margin slightly concave. Dorsal shield complete, pear-shaped (Fig. 5E, but in some females more rectangular), posterior margin concave, 608 (591-660) long and 470 (417-486) wide. D1 and L4 on humps. Medial margin of fourth coxal plates larger than medial margin of third coxal plates. Gonopore 105 long, without chitinous patches. Genital plates long, widened laterally (Fig. 5F). V2 on humps. Lengths of PI-PV: 32, 72, 52, 68, 50; palp as in male. Lengths of I-leg-4-6: 150, 152, 148. Lengths of IV-leg-4-6: 146, 180, 174.

REMARKS. The shape of the cauda and petiole will easily separate the new species from other species. The female is characterised by the shape of the genital plates.

Arrenurus (Megaluracarus) degeneratus
Viets, 1984 nov. comb.

Arrenurus (Megaluracarus) rostratus degeneratus K.O. Viets, 1984: 434; Smit, 1997: 246; Harvey, 1998: 144.

MATERIAL. *Western Australia*. ♂, ♀, pool upstream of Bell Gorge Falls, the Kimberley, 11 September 1998. 2 ♂, 2 ♀, Lily Creek Lagoon, Kununurra, 17 September 1998. 31 ♂, 9 ♀, Lake Kununurra, 10km SE of Kununurra, 19 September 1998.

REMARKS. Large differences can be found between *A. rostratus* Daday (and its new subspecies, see below) and *A. degeneratus*. The last species is larger, and both male and female of the two species differ quite strongly in the shape of the body. Moreover, *A. rostratus mutilus* subsp. nov. and *A. degeneratus* have been found at the same location (pool upstream of Bell Gorge Falls), and can therefore not belong to the same species. Therefore, an elevation in rank to species is proposed for *A. degeneratus*.

DISTRIBUTION. NT and WA. Harvey (1997) reported the species from Queensland. I assume that his record refers to Viets (1975) report of *A. rostratus* probably from Queensland. As the material in the Viets collection from

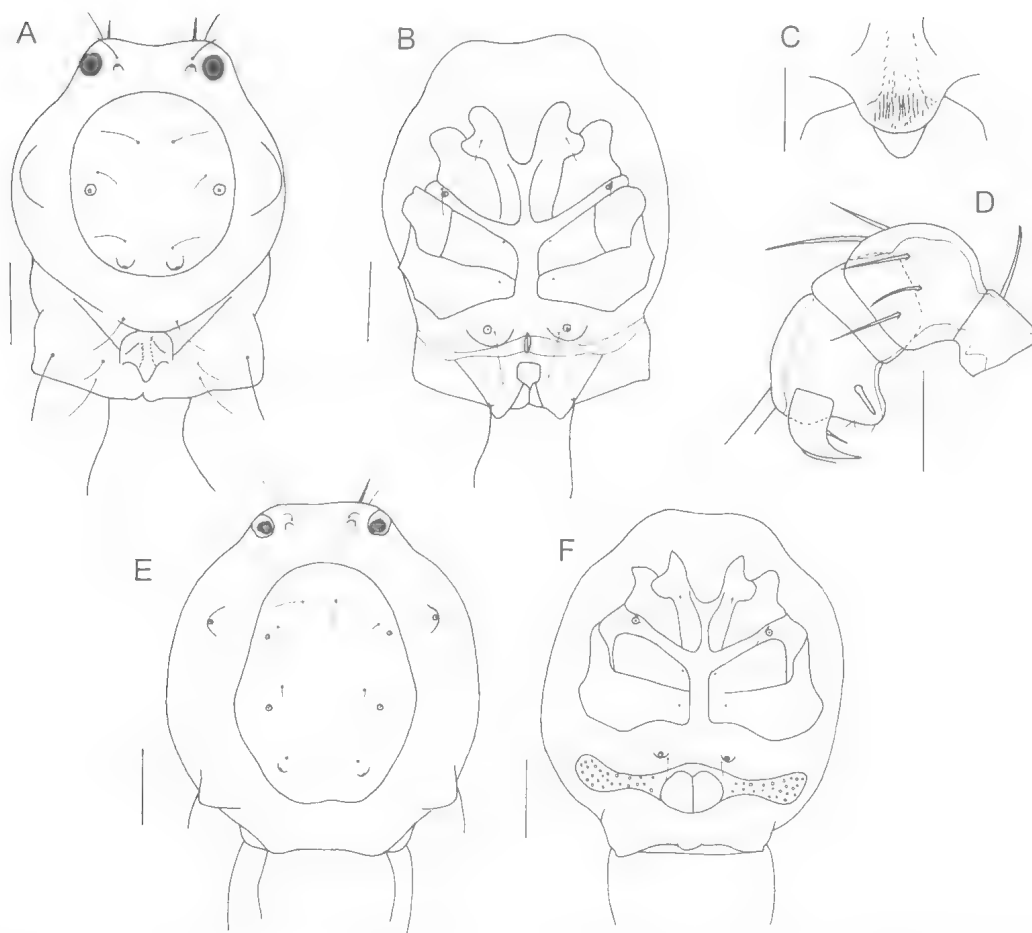


FIG. 5. *Arrenurus recticaudatus* sp. nov., holotype ♂: A, dorsal view; B, ventral view; C, detail of petiole; D, palp. *Arrenurus recticaudatus* sp. nov., paratype ♀; E, dorsal view; F, ventral view. Scale bars: A,B,E,F = 200 µm; C,D = 50 µm.

Queensland must be assigned to *A. rostratus mutilus*, I consider Harvey's record erroneous.

***Arrenurus (Megaluracarus) gilvus* Smit, 1997**

Arrenurus (Megaluracarus) gilvus Smit, 1997: 242; Harvey 1998: 144.

MATERIAL. *Western Australia.* 1 ♂, 5 ♀, pool Amalia Gorge, El Questro Station, 16 September 1998.

REMARKS. Some additional measurements and characters are: Male. Body 964 long, 518 wide. Female. Body 794-891 long, 680-713 wide. Dorsal furrow complete, dorsal shield 527-567 long, 462-502 wide. One aberrant female with much narrower genital plates, otherwise similar.

DISTRIBUTION. NT and WA.

***Arrenurus (Megaluracarus) harpagopalpus* Walter, 1929**

Arrenurus harpagopalpus Walter, 1929a: 252; Viets, 1981: 334; Smit, 1997: 259; Harvey, 1998: 144.

MATERIAL. *Queensland.* 2 ♂, 4 ♀, 1 nymph, shallow pool along road to Hanush Waterhole, Lakefield NP, 4 September 2000. 4 ♂, ♀, 2 nymphs, Low Lake, Lakefield NP, 5 September 2000.

DISTRIBUTION. Indonesia (Java), NT, NSW and QLD.

***Arrenurus (Megaluracarus) rostratus mutilus* subsp. nov. (Fig. 6)**

Arrenurus (Megaluracarus) spec A - Smit, 1992: 107.

ETYMOLOGY. For its truncated body.

MATERIAL. HOLOTYPE. ♀, Jack's Waterhole (along Gibb River Road), the Kimberley, WA, 14 September 1998 (WAMT42596). **PARATYPES.** 9♂, 13♀ (WAMT42597), 9♂, 14♀ (ZMAN type ACAR.0004.1-23.), same data as holotype. **OTHER MATERIAL.** *Queensland.* ♂, ♀, Stock Dam, Anakie, 18 July 1974, coll. B.V. Timms (slides SMF5656, 5655). ♀, pond N of Normanton, 14 August 1989. 3♂, 5♀, Lake Emma, Lakefield NP, 3 September 2000. 6♀, Low Lake, Lakefield NP, 5 September 2000. 2♂, ♀, swamp 9 km E of Musgrave, along road to Lakefield NP, 5 September 2000. *Western Australia.* ♂, ♀, Cockatoo Creek at crossing with Great Northern Highway, 8 September 1998. ♂, 2♀, pools upstream of Bell Gorge Falls, the Kimberley, 11 September 1998. ♀, pool downstream of Manning Gorge, at campground, the Kimberley, 12 September 1998. ♂, pool Amalia Gorge, El Questro Station, 16 September 1998. ♂, Fitzroy River, S of Fitzroy Crossing, 28 September 1998. *Northern Territory.* 3 ♀, Roper Valley Station spring, 12 July 1981, coll. B.V. Timms (slides SMF7444, 7445).

DIAGNOSIS. Body of female truncated.

DESCRIPTION. Male. Body 1029 (996-1061) long, 446 (429-454) wide, with a long pointed rostrum. Dorsal furrow complete, dorsal shield almost circular, 275 (275-284) in diameter; occasionally slightly longer than wide. Cauda long, narrow, widest part near posterior (Fig. 6A, B). Posterior part of cauda with a concavity. Gonopore 60 long. Genital plates long, narrow, reaching beyond lateral body margin. Lengths of PI-PV: 22, 54, 38, 62, 34; palp as in female. Lengths of I-leg-4-6: 106, 107, 152. Lengths of IV-leg-4-6: 188, 122, 150; IV-leg-4 without a spur.

Female. Body 875 (818-931) long, 591 (587-688) wide, yellowish-greenish, with a distinct rostrum anteriorly. Dorsal furrow incomplete, dorsal shield 421 (413-498) wide. Body posteriorly truncated, posterior margin straight to slightly concave (Fig. 6C). Shape of truncated posterior body part variable, specimens with a broader truncated part do occur (Fig. 6F). Medial distance of fourth coxal plates slightly smaller than width of one genital valve. Medial margin of fourth coxal plates larger than medial distance of third coxal plates. Gonopore 116 long and without chitinised patches. Genital field short, rounded and sloping posteriorly (Fig. 6D). However, specimens with a straight posterior margin of the genital plate can be found (Fig. 6G). Lengths of PI-PV: 22, 56, 42, 62, 38. PII with two short setae on medial side, PIV stocky (Fig. 6E). Lengths of I-leg-4-6: 112, 102, 136. Lengths of IV-leg-4-6: 150, 130, 136.

REMARKS. The female has a truncated posterior body part. Females of widespread *A. rostratus rostratus* Daday have a rounded posterior body part, which is not truncated. The male is not separable from the nominate form, but as all females collected so far belong to the new subspecies, all males are assigned to the new subspecies as well. Variation in the cauda is similar to that in *A. rostratus rostratus*.

Arrenurus (Megaluracarus) thienemanni
Viets, 1984

Arrenurus (Megaluracarus) thienemanni Viets, 1984: 432; Smit 1997: 243; Harvey 1998: 144.

MATERIAL. *Western Australia.* ♀, Fitzroy River, at crossing with Great Northern Highway, S of Derby, 8 September 1998. 10♂, 5♀, pool Lennard Gorge, Windjana Gorge National Park, the Kimberley, 10 September 1998. ♀, pool Lennard River, E side Windjana Gorge, Windjana Gorge National Park, the Kimberley, 10 September 1998. 5♂, 3♀, pool 3 km from Lennard Gorge, the Kimberley, 10 September 1998. 3♂, pool near Adcock Gorge, the Kimberley, 12 September 1998. 3♀, pool Manning Gorge Falls, the Kimberley, 13 September 1998. ♀, Jack's Waterhole, the Kimberley, 14 September 1998. 2♂, 18♀, pool Amalia Gorge, El Questro Station, the Kimberley, 16 September 1998. ♀, Middle Springs, W of Kununurra, 18 September 1998. ♂, ♀, Spillway Creek near Lake Argyle, 20 September 1998. ♂, Arthur Creek, at crossing with Great Northern Highway, the Kimberley, 23 September 1998. 3♂, pools in creek at Old Halls Creek, S of Halls Creek, 26 September 1998. 5♂, pool W of Tunnel Creek, Tunnel Creek National Park, 30 September 1998.

REMARKS. A character not previously reported is the very short rostrum of the males.

DISTRIBUTION. NT and WA.

Arrenurus (Megaluracarus) vanderpalae
Smit, 1992

Arrenurus (Megaluracarus) vanderpalae Smit, 1992: 109, 1997: 246; Harvey, 1998: 144.

MATERIAL. *Western Australia.* 2♂, 3♀, plunge pool Cathedral Gorge, Purnululu NP, 24 September 1998.

DISTRIBUTION. QLD and WA.

Arrenurus (Truncaturus) tasmanicus
Lundblad, 1941

Arrenurus (Truncaturus) tasmanicus Lundblad, 1941: 160; Lundblad 1947: 77; Smit, 1992: 110; Harvey, 1998: 144.

MATERIAL. *New South Wales.* 5 ♀, swamp no. 5, Myall Lakes National Park, 13 September 1977, coll. B.V. Timms (SMF6706-6708).

REMARKS. Kurt Viets erroneously identified these specimens as *A. depressus*, a species only

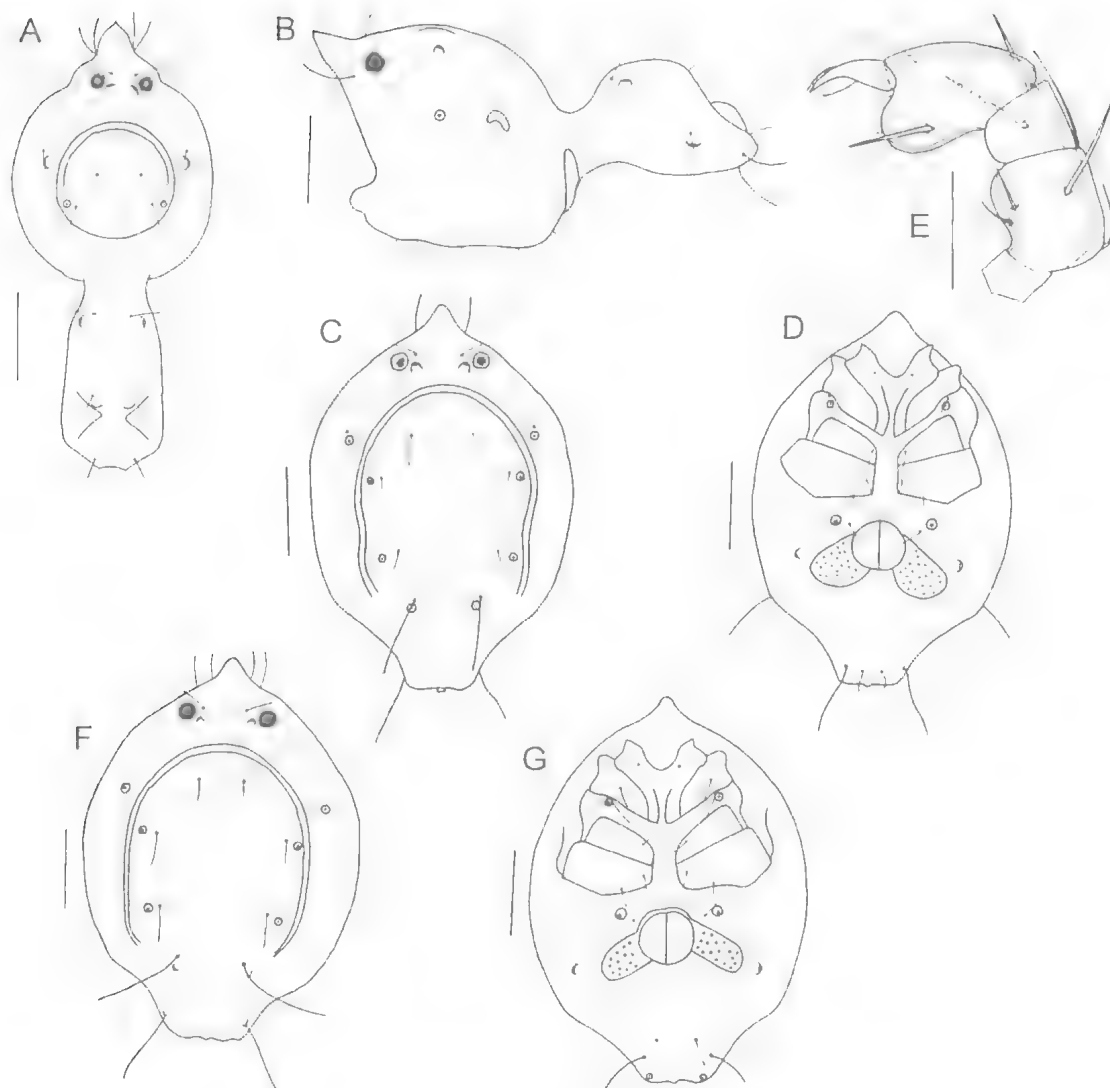


FIG. 6. *Arrenurus rostratus mutilus* subsp. nov., paratype ♂; A, dorsal view; B, lateral view. *Arrenurus rostratus mutilus* subsp. nov., holotype ♀; C, dorsal view; D, ventral view; E, palp. *Arrenurus rostratus mutilus* subsp. nov., paratype ♀; F, dorsal view; G, ventral view. Scale bars: A,B,C,D,F,G = 200µm; E, = 50µm.

known in New Caledonia. However, its genital plates are slightly bowed, while those of the NSW specimens are slightly contracted laterally.

DISTRIBUTION. TAS and NSW.

***Arrenurus (Rhinophoracarus) gracilipes*
Piersig, 1906**

Arrenurus (Rhinophoracarus) gracilipes Piersig, 1906: 370;
Smit, 1997: 251.

Rhinophoracarus gracilipes (Piersig): Viets, 1935: 2;
Lundblad, 1969: 392.

MATERIAL. *Queensland*. 3♂, 14♀, White Lily Lagoon, Lakefield NP, 4 September 2000. ♂, 4♀, Red Lily Lagoon, Lakefield NP, 4 September 2000. ♂, 4♀, pool along road to Hanush Waterhole, Lakefield NP, 4 September 2000. ♂, 2♀, Low Lake, Lakefield NP, 5 September 2000. ♂, swamp 9 km E of Musgrave, along road to Lakefield NP, 5 September 2000. 8♀, billabong W of Wenlock River, at crossing with road to Iron RangeNP, 10 September 2000. *Western Australia*. 5♀, Cockatoo Creek at crossing with Great Northern Highway, 8 September 1998. 2♀, Lily Creek Lagoon, Kununurra, 17 September 2000. ♀, Lake Kununurra, 10km SE of Kununurra, 19 September 1998.

DISTRIBUTION. Burma, India, Indonesia, QLD, WA.

Arrenurus (Dividuracarus) gereckeii Smit
(Fig. 7)

Arrenurus (Dividuracarus) gereckeii Smit, 1997: 255;
Harvey, 1998: 144.

MATERIAL. *Western Australia.* 8 ♂, 6 ♀, Arthur Creek, at crossing with Great Northern Highway, 23 September 1998. ♂, plunge pool Frog Hole Gorge. Purnululu NP, 23 September 1998. *New South Wales.* ♀, Lake Hiawatha, 10 August 1975, coll. B.V. Timms (SMF6192). ♂, Lake Hiawatha, 17 March 1977, coll. B.V. Timms (SMF6435). *Northern Territory.* ♂ (not sclerotised), Magela Creek floodplain, Jabiluka Billabong, 19 January 1979, coll. R. Tait (SMF7121). ♀, Magela Creek floodplain, Island Billabong, 21 May 1979, coll. R. Tait (SMF7161). ♀, Magela Creek floodplain, Buffalo Billabong, 22 May 1979, coll. R. Tait (SMF7113). ♂, Magela Creek floodplain, Ja Ja Billabong, 23 May 1979, coll. R. Tait (SMF7171). 3 ♀, Magela Creek floodplain, Winnurra Billabong, 23 July 1979, coll. R. Tait (SMF 7193-7195). ♂, 2 ♀, Magela Creek floodplain, Winnurra Billabong, 27 September 1979, coll. R. Tait (SMF7202- 7204). ♂, 3 ♀, Magela Creek floodplain, Winnurra Billabong, 15 November 1979, coll. R. Tait (SMF7214- 7217).

DESCRIPTION. Male. 996-1105 long, 745-810 wide. Female. Body 1158 (1126-1255) long, 988 (923-1037) wide, greenish, with slightly concave anterior margin, truncated anteriorly and posteriorly. D1 and L4 on small humps. Dorsal furrow complete, dorsal shield 721 long, 664 wide. Medial distance of fourth coxal plates large; fourth coxal plates almost without a medial margin or with a short medial margin. Gonopore extended laterally. Genital plates directed perpendicularly or slightly bowed to lateral body margin, short, about 1.5 times as long as wide (Fig. 7). Lengths of PI-PV: 38, 94, 56, 103, 51; palp as in male. Lengths of I-leg-4-6: 140, 128, 106. Lengths of IV-leg-4-6: 235, 227, 196. Third and fourth legs with numerous swimming setae.

REMARKS. The female which has not been described previously, has an unusual gonopore, with lateral extension not found in any other member of the genus.

DISTRIBUTION. QLD, WA and NSW.

Arrenurus (Dividuracarus) tripartitus Smit,
1997

Arrenurus (Dividuracarus) tripartitus Smit, 1997: 255;
Harvey, 1998: 144.

MATERIAL. *Western Australia.* ♀, pool Joffre Gorge, Hamersley Range NP, 13 August 1994.

DISTRIBUTION. QLD and WA.

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LITERATURE CITED

- COOK, D.R. 1967. Water mites from India. *Memoirs of the American Entomological Institute* 9: 1-411.
- DADAY, E. VON 1898a. Édesvízi mikroskopi állatok Ceylonból. *Matematikai és Természettudományi, Értesítő* 16: 89-100.
- 1898b. Mikroskopische Süßwasserthiere aus Ceylon. *Természettudományi Füzetek, Anhangsheft* 21: 1-123.
- FERNANDO, C.H. 1963. A guide to the freshwater fauna of Ceylon. *Bulletin of the Fisheries Research Station, Ceylon* 16: 29-38.
1990. The freshwater fauna and fisheries of Sri Lanka. A collection of published papers by C.H. Fernando and collaborators (1962-1980), with taxonomic and common name indexes. *Suborder Hydracarina*, pp. 268-273. (Natural Resources, Energy and Science Authority of Sri Lanka: Colombo).
- GLEDHILL, T. & WILES, P.R. 1997. Water-mites (Acari: Hydrachnidia) from Sri Lanka with descriptions of a new genus and two new species. *Archiv für Hydrobiologie, Supplement* 107: 513-539.
- HARVEY, M.S. 1998. The Australian water mites. A guide to families and genera. *Monographs on Invertebrate Taxonomy* 4. (CSIRO Publishing: Collingwood).
- IMAMURA, T. 1953a. Some water-mites from Hiroshima Prefecture. *Journal of the Faculty of Science of the Hokkaido University* 11: 193-260.
- 1953b. Some stenophilous water-mites from Hyogo Prefecture. *Journal of the Faculty of Science of the Hokkaido University, Zoology* 11: 261-276.
- 1953c. Water-mites from Gifu Prefecture. *Journal of the Faculty of Science of the Hokkaido University, Zoology* 11: 411-471.
1954. Some stenophilous water-mites from Niigata Prefecture. *Journal of Hokkaido Gakugei University, Section B, Supplement* 1: 149-164.
1956. Water-mites from lakes Kasumigaura and Kitaura. *Bulletin of the Faculty of Liberty and Arts, Ibaraku University* 6: 23-26.
1961. Water-mites (Hydrachnellae), mainly in subterranean waters, from the Ryu-Kyu Islands. *Acarologia* 3: 48-59.
- JIN DAOCHAO & WILES, R. 1996. New species of *Arrenurus* Dugès (Acari: Hydrachnidia:

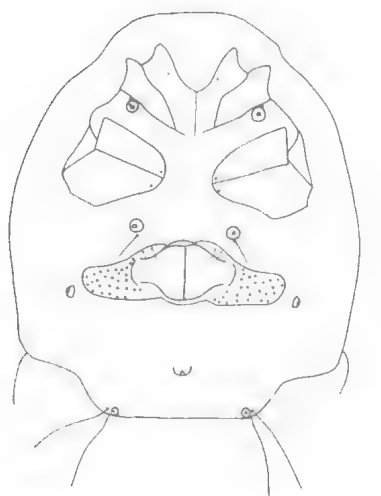


FIG. 7. *Arrenurus gereckeï*, Smit, ♀, ventral view. Scale bar = 200µm.

- Arrenuridae) from China and first records of watermites from Laos. *Acarologia* 37: 317-344.
- LUNDBLAD, O. 1941. Neue Wassermilben aus Amerika, Afrika, Asien und Australien. *Zoologischer Anzeiger* 133: 155-160.
1947. Zur Kenntnis Australischer Wassermilben. *Arkiv för Zoologie* 40A: 1-82.
- MARSHALL, R. 1921. New species and collections of Arrhenuri: 1921. *Transactions of the American microscopical Society* 40: 168-176.
1928. Water mites from China. *Transactions of the Wisconsin Academy of Sciences, Arts and Letters* 23: 601-609.
- MENDIS, A.S. & FERNANDO, C.H. 1962. A guide to the freshwater fauna of Ceylon. *Bulletin of the Fisheries Research Station, Ceylon* 12: 1-160.
- MIYAZAKI, I. 1935. On a water mite parasitic on *Anopheles*. *Botany & Zoology, Tokyo* 3: 725-729. (in Japanese)
- PIERSIG, R. & LOHMANN, H. 1901. Acarina, Hydrachnidae and Halacaridae. *Das Tierreich* 13: 1-336.
- PIERSIG, R. 1906. Über Süßwasser-Acarinen von Hinterindien, Sumatra, Java und den Sandwich-Inseln. (Reise von Dr. Walter Volz.). *Zoologische Jahrbücher, Abteilung für Systematik* 23: 321-394.
- REISEN, W.K. & MULLEN, G.R. 1978. Ecological observations on acarine associates (Acari) of Pakistan mosquitos (Diptera: Culicidae). *Environmental Entomology* 7: 769-776.
- SMIT, H. 1992. Water mites from New South Wales and Queensland, Australia. *Tijdschrift voor Entomologie* 135: 91-112.
1997. Australian water mites of the genus *Arrenurus*, with the description of 12 new species, from northern and western Australia (Acari: Hydrachnellae: Arrenuridae). *Records of the Western Australian Museum* 18: 233-261.
1999. New species of the water mite genus *Arrenurus* from eastern Australia (Acari: Hydrachnidia: Arrenuridae). *Memoirs of Museum Victoria* 57: 225-236.
- UCHIDA, T. & MIYAZAKI, I. 1935. Life-history of a water-mite parasitic on *Anopheles*. *Proceedings of the Imperial Academy (of Japan)* 11: 73-76.
- UCHIDA, T. 1937. Water mites from Kyushu. *Bulletin of the biogeographical Society* 7: 9-29.
- UCHIDA, T. & IMAMURA, T. 1951. Some water mites from China. *Journal of Science, Hokkaido University, Sapporo, serie VI, Zoology* 10: 324-358.
- VIETS, K. 1926. Fauna sumatrensis. (Beitrag Nr. 15). Hydracarina. *Entomologische Mitteilungen, Berlin* 15: 100-102.
1927. Wassermilben von Hinterindien. *Zoologischer Anzeiger* 73: 315-322.
1929. Watermites from the Malay Peninsula. *Journal of the Federated Malay States Museums* 14: 397.
1935. Die Wassermilben von Sumatra, Java und Bali nach den Ergebnissen der Deutschen Limnologischen Sunda-Expedition. *Archiv für Hydrobiologie, Supplement* 14: 1-113.
- VIETS, K.O. 1959. Wassermilben (Hydrachnellae) aus dem indo-australischen Faunengebiet. *Archiv für Hydrobiologie* 55: 415-428.
1973. Results of the Austrian-Ceylonese Hydrobiological Mission 1970 of the 1st Zoological Institute, University of Vienna (Austria) and Department of Zoology, Vidyalankara University of Ceylon, Kelaniya, Ceylon. Part III. Über einige Wassermilben aus Ceylon (Hydrachnellae, Acari). *Bulletin of the Fisheries Research Station, Ceylon* 23: 101-111.
- WALTER, C. 1923. Hydrobiologische Beiträge aus China. Nach Dr. H. Weigolds Material von den Stütznerschen Expeditionen und aus China. Hydracarina. Zugleich ein Beitrag zur Frage der Hautatmung bei *Arrhenurus*-Arten. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 11: 193-201.
1928. Zur Kenntnis der Mikrofauna von British Indien. *Records of the Indian Museum* 30: 57-108.
- 1929a. Hydracarininen aus Java. *Treubia* 11: 211-273.
- 1929b. Revision der von E. von Daday beschriebenen Hydracarininen von Ceylon. *Annales Musei Nationalis Hungarici* 26: 251-268.
- WILES, P.R. 1997. The homology of glands and glandularia in the water mites (Acari: Hydrachnidia). *Journal of Natural History* 31: 1237-1251.

PREVALENCE OF ULCERATIVE DISEASE IN FREE-RANGING KREFFT'S TURTLE

A.D. TUCKER, W.R. KELLY, C.J. LIMPUS, T.E. PRIEST AND F. GUARINO

Tucker, A.D., Kelly, W.R., Limpus, C.J., Priest, T.E. & Guarino, F. 2002 5 31: Prevalence of ulcerative disease in free-ranging Krefft's Turtle. *Memoirs of the Queensland Museum* 48(1): 233-238. Brisbane. ISSN 0079-8835.

Clinical evidence is documented for an ulcerative skin disease of unknown cause which is prevalent in a population of Krefft's turtles (*Emydura krefftii*) in east-central Queensland. The population in Callide Dam near Biloela was the sole known focus of disease, despite intensive surveys of surrounding catchments. Fresh or regressing skin lesions occurred in 39% of 869 turtles caught over 7 sampling occasions (range 25-84%). We document disease prevalence within the population and preliminary histopathological findings. Similar infectious diseases in other aquatic vertebrates are reviewed. □ *Ulcer; disease; turtle, Emydura krefftii*.

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There is an increasing trend in numbers of reports of disease in chelonians; emerging infectious diseases are now known for all the major groups, including sea turtles (viral fibropapillomas), freshwater turtles (ulcerative shell necrosis) and land tortoises (upper respiratory tract infections) (Herbst, 1994; Lovich et al., 1996; Garner et al., 1997; Berry, 1997; Ernst et al., 1999). To reiterate Jacobsen (1997), it is imperative to distinguish whether recently documented diseases reflect an onset of degraded environmental conditions (Cann, 1993), biomagnification of chemical toxicants in the environment (Ernst, 1997) or an increase of interest in these animals.

There is limited awareness about the health status of Australian chelids, despite a burgeoning concern for the status of turtle populations elsewhere (Ernst, 1997). Cann (1993, 1998) drew attention to the *Elseya bellei* populations of the Namoi River, NSW which suffer from blindness, and also an *Emydura* population in Victoria which declined at a time of toxic algal blooms (Cribb, 1991). Apart from these qualitative observations, we are not aware of any quantitative accounts of disease in free-ranging freshwater turtles in Australia. Nevertheless, reports are received sporadically about localised die-offs of freshwater turtles in SE Queensland. Since 1995, mass mortalities within isolated small farm impoundments were noted with *Elseya latisternum* and *E. signata* in the Brisbane and Pine Rivers catchments and with *Chelodina longicollis* in the

upper Darling Downs Catchment as well as the upper Dawson River (C. Limpus unpublished data). It is unknown if disease, contamination or natural environmental variation is implicated since none of the die-offs occurred in conjunction with fish kills. Timely documentation and follow-up are required if forensics are to be useful in such episodes.

This paper documents clinical, epidemiological and pathological features of a skin disease of unknown cause which became prevalent in a single population of Krefft's turtles (*Emydura krefftii*) in east-central Queensland. This population is the sole known focus of disease at present, despite intensive surveys of the surrounding catchments.

METHODS

Surveys of the Fitzroy, Kolan, Burnett and Mary River were initiated by the Queensland Parks and Wildlife Service in 1997-1999 to assess the effects of dams and weirs on freshwater turtle populations (Tucker, 2000). The only population that displayed evidence of disease (among >10,000 turtles collected from 28 riverine sites and 26 dam sites) was at Callide Dam (24°21.793S, 150°38.650E; 10km E of Biloela). Following the first recognition of the disease in July 1998, we conducted follow-up surveys at irregular intervals over the next year to monitor temporal variation in prevalence of clinical signs (survey dates are given in Table 1).

TABLE 1. Summary of Krefft's turtles that displayed symptoms of active or healing ulcerations when encountered during surveys of Callide Dam. Note: total turtles sampled includes 5 recaptured turtles, of which 3 had new ulcers when recaptured.

Date of sampling	Ulcers or recent scars present	Total turtles sampled	% diseased
11/7/98	72	220	32.7
30.8/98	42	70	58.3
15/12/98	21	25	84.0
17/2/99	65	242	26.9
25/2/99	88	180	48.9
15/4/99	49	116	42.2
27/5/99	4	16	25.0
Overall	341	869	39.2

STUDY SITE. Callide Dam impounds Callide Creek to provide cooling water to an adjacent coal-fired power generating plant situated immediately to the northwest and for irrigation of an intensive cotton-growing industry of the surrounding region. To the north is one of the Callide coalfields that extract low-grade sulphur coal for the power plant. The large cooling towers are monitored to strict environmental standards so that any water taken from Callide Dam for cooling or furnace ash washing is self-contained and recirculated within settling ponds on the plant grounds. Some surface runoff from the plant and mine may enter the lake. However, the role of groundwater transport or agricultural runoff is not monitored.

Water quality of Callide Dam is tested by a local Queensland Dept of Natural Resources laboratory in Biloela (Allen, 1982). The waters that feed Callide are pumped uphill from Awoonga Dam, a coastal catchment separated by a low mountain range. The water pH is 7.7-7.9 as it enters Callide Creek. The lake stratifies and has documented high levels of nutrients. Fisheries surveys in Callide Dam have recorded pH of 8.0-8.5 consistently over the past decade (P. Long-QDPI, unpubl. data).

STUDY ANIMALS. Krefft's turtle (*E. krefftii*) is a common chelid turtle in rivers, reservoirs and farm ponds of SE Queensland (Cann, 1998). The Fitzroy region hosts a high biodiversity of turtle species (*E. krefftii*, *Rheodytes leukops*, *E. latisternum*, *Elseya* sp., *Chelodina expansa*, *C. longicollis* and *C. novaeguinea*, with a hybrid zone between the latter two). Because *E. krefftii* is the least specialised of these turtle species in its

habitat and diet, it predominates in permanent aquatic habitats (Tucker, 2000).

The *E. krefftii* in Callide Dam are distributed at high density in the shallower margins of the lake, where waters are regularly anoxic and thermally stratified (QPWS, unpubl. data). These conditions may be exacerbated because Callide Dam has remained at low storage levels for many years (QDNR water storage reports).

SPECIMEN PROCESSING. Turtles were obtained on two initial occasions by seining and thereafter by baited crab traps. Turtles were kept shaded in mesh bags or bins during processing. All turtles were returned to the vicinity of capture within 24 hrs, except for specimens that died during processing or that were retained for necropsy. We took standard measurements of length (carapace and plastron length were measured to the nearest 1mm with callipers) and weight (measured to the nearest 1g on an electronic balance) of each turtle. A body condition index was assessed from the residuals for a regression of carapace length to mass by the equation $mass = a*(SVL)^b$.

In the Callide population, adult turtles (carapaces > 20cm) were reliably sexed by dimorphism of the tail. Males have a thickened elongate tail with the vent position posterior to the rear margin of the carapace; females have a relatively short tapered tail with the vent not extending beyond the rear margin of the carapace. For turtles < 20cm that displayed no dimorphism, we viewed the gonads directly via laparoscopy to determine sex (detailed methods given in Limpus et al., 2002). Each turtle was individually marked by a numbered metal tag inserted in the webbing of the rear foot. Each turtle was inspected visually for ulcers on the skin of the neck and shoulder region. Ulcers were coded as 0, 1, or 2 respectively for no evidence, active ulceration, or remnant scar tissue from what was assumed to have been a previous ulcer. Recaptures of tagged individuals that had been affected previously were followed to record cases of ulcer progression or recovery.

On 17 February 1999, 6.2% of the sampled animals (n=15/242) died while being held for processing. Deaths were from 4.5% (4/88 of males, 7.7% (11/143) of females, and no juveniles. Such mortality had not been recorded elsewhere and there had been no significant change in our processing procedures, which had previously resulted in negligible mortality. We viewed the mortality with apprehension because

of the external ulcers and what we subjectively assessed as poor condition in the population. The 15 carcasses were frozen for later examination. Detailed pathological examination was not performed on these specimens due to the freeze-thaw artifact.

We returned on 25 February to collect a sample of live turtles with both symptomatic and normal appearance. Specimens were transported to the Veterinary Pathology lab at University of Queensland where they were submitted for clinical, necropsy and histopathological examination on 26 February.

Complete necropsy dissection was performed on one normal and 4 turtles with skin ulcers, immediately after euthanasia by intravenous injection of pentobarbitone sodium solution. Haematoxylin and eosin-stained sections of formalin-fixed skin and liver tissue were cut from paraffin-embedded blocks.

Dietary samples were obtained by stomach-flushing 10 turtles on 15 December 1998. Stomach samples were preserved in 70% ethanol and identified later with a dissecting microscope and field guides. Prey species were quantified by percent occurrence.

RESULTS

Fresh or healed skin ulcers occurred in 39% of 869 turtles caught over 7 sampling occasions (range 25-84%) (Table 1). Affected turtles had fresh or healing ulcers on the dorsal aspect of the neck or shoulder region. Lesions were equally common in males, females, and juveniles. Recaptures of individual turtles were sparse ($n=5$), but of these, 2 turtles remained unaffected, and 3 turtles had become ulcerated between captures. Recapture numbers were insufficient to assess the outcome of the disease (healing or progression), given that recapture was dependant on survival as well as the probability of recapture. An alternative was to contrast the percentages of turtles with active and regressive ulcers (39%, Table 1) to those which only had active ulcers (18%, Table 2). A 21% difference was a representative index of turtles with ulcers that would be expected to regress.

Analysis of variance indicated that affected males, females, and juveniles had a significantly lower length ($F=71$, $P=0.0001$), mass ($F=141$, $P<0.001$), and mass/length ratio ($F=109$, $p<0.0001$) than unaffected individuals (Table 2). Residuals from the power function relating length to body mass ($\text{mass} = a*(\text{SVL})^b$; $a=$

TABLE 2. Comparisons of length, mass, and condition for 'normal' and affected *Emydura krefftii* at Callide Dam. Table values are means with 1 s.e. in parenthesis. Sex is abbreviated as F-female, M-male, I-immature with a - or + sign indicating absence (82%) or presence (18%) of lesions, respectively. Note: mass data were unavailable on 20 turtles (for logistic reasons), so sample sizes differ from Table 1. Negative residuals in the right column indicated animals in poorer body conditions than expected for the population, and were calculated as a body condition index from regressions of body length to mass given in Fig. 1.

Turtle	N	Length (cm)	Mass (kg)	Ratio kg/cm	Body Condition (residual)
F-	416	24.05 (0.14)	1.707 (0.027)	0.069 (0.001)	0.249 (0.055)
F+	80	23.15 (0.39)	1.533 (0.068)	0.063 (0.002)	-0.062 (0.126)
M-	237	21.69 (0.19)	1.173 (0.027)	0.052 (0.001)	-0.334 (0.049)
M+	63	20.85 (0.40)	1.043 (0.055)	0.048 (0.001)	-0.325 (0.081)
I-	43	12.58 (0.49)	0.272 (0.029)	0.019 (0.001)	0.002 (0.029)
I+	10	12.72 (0.48)	0.239 (0.021)	0.018 (0.001)	-0.053 (0.044)

0.000088775 , $s.e. = 0.0000101866$; $b=3.08146$, $s.e.=0.035723$) indicated whether an individual was greater than or less than the population standard for animals of given size; for the Callide turtles, these responses were unique by sex (Table 2). Unaffected females had positive residuals relative to affected females, both groups of males had negative residuals of similar magnitude, while both groups of juveniles displayed residuals not significantly different from the baseline. In other words, only unaffected females weighed more than expected for their respective size. Plots of $\ln(\text{SVL})$ against $\ln(\text{mass})$ indicated that the residuals were not a result of different slopes or intercepts by sex, as all plots coincided on a single regression line. However, without knowing the contributions of muscle, oedema fluid and fat to body weight of these live turtles, we cannot say whether a heavier than average turtle for its size (noted by a positive residual) resulted from fairly extensive fat deposits or some pathology such as oedema or ascites, etc.

The ten stomach samples revealed that *E. krefftii* foraged across multiple trophic levels in the reservoir. Six turtles consumed submerged aquatic plants (*Myriophyllum* sp., *Ceratophyllum* sp.), 5 ate inundated terrestrial grasses, 4 consumed bivalves, 3 scavenged fish, 3 ingested

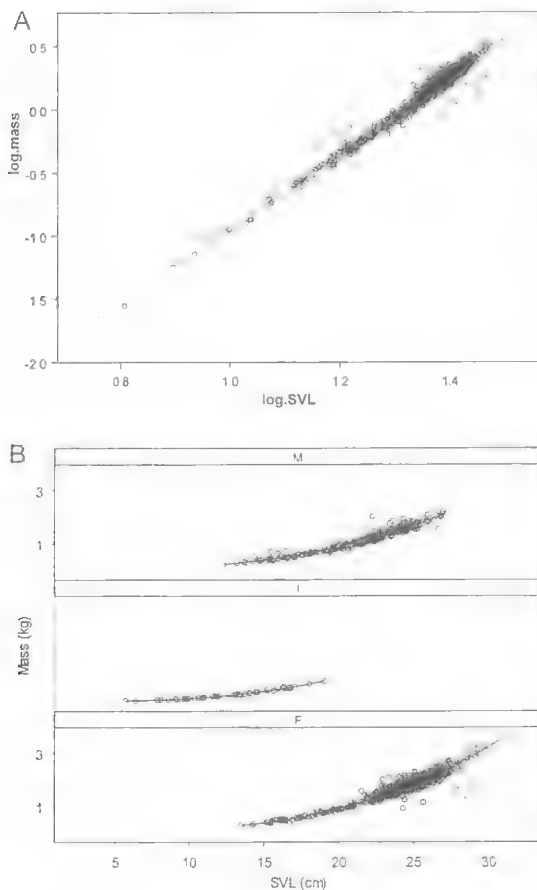


FIG. 1. A, coincidence of all points to a common regression line, regardless of sex. B, points conditioned by sex to indicate relationship of length to body mass ($\text{mass} = a(\text{SVL})^b$; $a = 0.000088775$, $\text{s.e.} = 0.0000101866$; $b = 3.08146$, $\text{s.e.} = 0.035723$) for Krefft's turtles (*E. krefftii*) in Callide Dam.

gum leaves as windfall, and 2 had consumed filamentous algae. Although aquatic plants are often ingested incidentally as turtles consume aquatic insect larvae, there were no traces of larvae found in the samples.

Clinical examination of 3 males and 1 female revealed single small sunken, puckered circular scars ranging from 3–5mm diameter on the dorsal neck skin just behind the head of each animal. All animals appeared vigorous. Necropsy revealed minimal scarring of the soft tissues beneath the skin lesions. All animals had adequate internal fat reserves and there were no gross abnormalities apparent at necropsy.

Histological examination confirmed that the

skin lesions were ulcers, covered by a dense diphtheritic membrane, overlying a fairly narrow zone of low-grade sub-acute inflammation. These ulcers were at more or less the same stage of resolution and did not appear to show a progression toward deeper infection. The cause of these ulcers was not apparent: there was no evidence in these sections of superficial or deep fungal invasion. The only other tissue examined histologically was liver, which showed marked fat accumulation in hepatocytes, and was judged to be normal, since the liver from the non-ulcerated animal was similar to those of the ulcerated turtles.

DISCUSSION

In summary, a previously unrecognised focal ulcerative skin disease has been recognised as occurring in *E. krefftii* in a single water impoundment over a two-year period. At the beginning of this period there was an unexplained mortality of 6% in a batch of recently-captured *E. krefftii*, but the cause of this mortality was not determined, nor was it established that there was any connection between the ulcerative disease and the mortality. Disease expression was variable over the year, but the irregular sampling protocol was insufficient to detect any seasonality in the condition (this investigation was during a regional survey into the effects of river regulation on freshwater turtle ecology (Tucker, 2000)).

The skin lesions of affected *E. krefftii* were only superficially similar to septicemic cutaneous ulcerative disease, which in aquatic turtles is characterised by cutaneous ulceration, anorexia, lethargy, and late in the course of the disease, hepatic necrosis, paralysis, and death (Frye, 1981). The infection is associated with the bacterium *Citrobacter freundii* and soft-shelled turtles (Trionychidae) are the group most frequently reported with the infection (Kaplan, 1957). However, such bacterial infections are most often secondarily associated with dermal abrasion of the plastron during handling of wild turtles or abrasions on captive turtles (Frye, 1981). The history and location of ulcers on the wild *E. krefftii* was inconsistent with abrasions due to capture. Several fungi are associated with lesions of the integument in aquatic chelonians, but keratin of the carapace is affected (Lovich et al., 1996; Garner et al., 1997) rather than dermis, as for example, *Basidiobolus ranarum* (Nickerson & Hutchinson, 1971). Another aquatic disease with clinical signs of ulcerative

mycosis is the pathogenic fungus *Mucor amphibiorum* (Munday et al., 1998), although this has not been reported for turtles. However, no fungal hyphae were noted in the histological sections so thus far fungal infection has not been implicated with the disease at Callide Dam.

Apart from bacterial and fungal agents, viral diseases pose threats to wildlife health. A recent review of emerging infectious disease in animals notes that ranaviruses, herpesviruses, and iridoviruses are common in aquatic organisms (Daszek et al., 1999).

Because the waters of Callide Dam are not used as a potable water source, limited data are collected on water conditions beyond biological oxygen demand or cyano-bacteria counts. Basic water pH (Allen, 1982) and lack of elevated sulphates or sulphites would seem to preclude links to acidic runoff conditions. That might rule out several fish diseases (such as red spot, when cutaneous ulcers are evident) that develop seasonally. Aromatic hydrocarbons, another potent skin irritant, are not monitored nor is there any systematic screening for pesticide compounds from local agricultural runoff (DNR Water Resources, pers. comm.).

Effective turtle conservation includes a recognition and proactive monitoring of threats (Klemens, 2000). Little is known about the immune systems of reptiles in general (Cooper et al., 1985) and the present knowledge of aquatic turtle diseases is derived principally from captive turtles as opposed to wild populations. Thus further study of Callide turtles may provide insight on disease processes in other free-ranging turtles. Conditions of high population density, low storage levels that create food-depleted conditions, highly stratified, anoxic water quality, and elevated levels of cyanobacteria or eutrophic conditions may be conducive to disease expression and transmission in aquatic turtles.

The health status of turtle populations is a vital concern because their life histories are poorly buffered against incidental mortality of later life history stages (Heppell, 1998), as in this case for adult females. Further investigation is needed to determine whether a disease of Callide *E. krefftii* might be transmitted to other aquatic species of the Fitzroy catchment. As the endemic Fitzroy Turtle (*Rheodytes leukops*) and an undescribed species of *Elseya* sp. are of specific conservation concern in the Fitzroy Catchment, measures may be warranted to contain a presently uncharacterised disease. If an infection cause is established

for the condition, precautions may include preventive quarantine of Callide turtles (whether taken during fishing contests or for pets) and disinfection of equipment after boating or trapping in the area. Turtles might also serve as active vectors since turtle movements during droughts are directed toward deeper reaches of river or overland to remnant water bodies (Cann, 1998). Furthermore, turtles may be flushed downstream during reservoir overflows. Such conditions have potential to readily disperse diseased individuals beyond the confines of Callide Dam.

Future studies are confronted by two major challenges: to determine the aetiology and pathogenesis of a new disease and whether it poses a disease risk to other aquatic species. A first step is to study turtles at earlier stages of the disease. Such investigations should include attempts to isolate pathogens from acutely affected individuals, followed by transmission trials of candidate isolates. Further work should be directed at determining the outcome (death, breeding compromise or recovery, etc) of the uncharacterised disease.

ACKNOWLEDGEMENTS

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LITERATURE CITED

- ALLEN, L. 1982. An assessment of the spatial and temporal variations of physico-chemical parameters in a central Queensland Water Impoundment. (Queensland Department of Natural Resources: Brisbane).
- BERRY, K.H. 1997. Demographic consequences of disease in two desert tortoise populations in California, USA. Pp. 91-99. In, Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles - an International Conference. (New York Turtle and Tortoise Society: New York).

- CANN, J. 1993. Do not take our freshwater turtles for granted. Pp. 363-365. In Lunney, D. & Ayers, D. (eds) *Herpetology in Australia, a diverse discipline*. Transactions of the Royal Zoological Society of New South Wales, (Surrey Beatty: Chipping Norton).
1998. *Freshwater Turtles of Australia*. (Beaumont Publishing: Singapore).
- COOPER, W.L., KLEMPAU, A.E. & ZAPATA, A.G. 1985. Reptilian immunity. Pp. 599-678. In Gans, C., Billett, F. & Maderson, P.F.A. (eds) *Biology of the Reptilia*. Vol. 14. development. (J. Wiley & Sons: New York).
- CRIBB, T. 1991. Death blooms in artificial paradise. *The Weekend Australian*. Aug. 3-4.
- DASZAK, P., BERGER, L., CUNNINGHAM, A.A., HYATT, A.D., GREEN, D.E. & SPEARE, R. 1999. Emerging infectious diseases and amphibian population declines. *Emerging Infectious Diseases* 5: 735-748.
- DODD, C.K. 1988. Disease and population declines in the flattened musk turtle *Sternotherus depressus*. *American Midland Naturalist* 119: 394-401.
- ERNST, C.H. 1997. Turtles of the United States: overview and prospects for the future. Pp. 27-31. In Tynning, T.F. (ed.) *Status and conservation of turtles of the northeastern United States*. (Serpent's Tale, Lanesboro: Minnesota).
- ERNST, C.H., AKRE, T.S.B., WILGENBUSCH, J.C., WILSON, T.P. & MILLS, K. 1999. Shell disease in turtles of the Rappahannock River, Virginia. *Herpetological Review* 30: 214-215.
- FRYE, F.L. 1981. *Biomedical and surgical aspects of captive reptile husbandry*. (Veterinary Medicine Publishing Company: Edwards, Kansas).
- GARNER, M.M., HERRINTSON, R., HOWERTH, M.E.W., HOMER, B.L., NETTLES, V.F., ISAZA, R., SHOTTS, E.B. Jr and JACOBSON, E.R. 1997. Shell disease in river cooters (*Pseudemys concinna*), and yellow-bellied turtles (*Trachemys scripta*) in a Georgia (USA) lake. *Journal of Wildlife Disease* 33: 78-86.
- HEPPELL, S.S. 1998. Application of life-history theory and population model analysis to turtle conservation. *Copeia* 1998: 367-375.
- HERBST, L.H. 1994. Fibropapillomatosis of marine turtles. *Annual Review of Fishery Diseases* 4: 389-425.
- JACOBSON, E.R. 1997. Diseases in wild populations of turtles and tortoises: the chelonian charisma vs coincidence conundrum. Pp. 87-90. In: *Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles-an International Conference*. (New York Turtle and Tortoise Society: New York).
- KAPLAN, H.M. 1957. Septicemic, cutaneous ulcerative disease of turtles. *Proceedings Animal Care Panel* 7: 273-277.
- KLEMENS, M.W. (ed.) 2000. *Turtle conservation*. (Smithsonian Institution Press: Washington DC).
- LIMPUS, C.J., LIMPUS, D.J. & HAMANN, M. 2002. Freshwater turtle populations in the area to be flooded by the Walla Weir, Burnett River. *Memoirs of the Queensland Museum* 48: 155-168.
- LOVICH, J.E., GOTTE, S.E., ERNST, C.H., HARSHBARGER, J.C., LAEMMERZAHIL, A.F. & GIBBONS, J.W. 1996. Prevalence and histopathology of shell disease in turtles from Lake Blackshear, Georgia. *Journal of Wildlife Disease* 32: 259-265.
- MUNDAY, B.L., WHITTINGTON, R.J. & STEWART, N.J. 1998. Disease conditions and subclinical infections of the platypus (*Ornithorhynchus anatinus*). *Philosophical Transactions Royal Society of London B* 353: 1093-1099.
- NICKERSON, M.A. & HUTCHINSON, J.A. 1971. The distribution of the fungus *Basidiobolus ranarum* Eidam in fish, amphibians and reptiles. *American Midland Naturalist* 86: 500-502.
- TUCKER, A.D. 2000. Cumulative impacts of dams and weirs on freshwater turtle populations of the Fitzroy, Kolan, Burnett, and Mary River catchments. Queensland Parks and Wildlife Service, research report.
- WALLACH, J.D. 1975. The pathogenesis and etiology of ulcerative shell disease in turtles. *Journal of Zoo Animal Medicine* 6: 11-13.
- WILES, M. & RAND, T.G. 1987. Integumental ulcerative disease in a loggerhead turtle *Caretta caretta* at the Bermuda Aquarium: microbiology and histopathology. *Diseases of Aquatic Organisms* 3: 85-90.

MORPHOLOGY-BASED REVISION OF *MUREXIA* AND *ANTECHINUS* (MARSUPIALIA: DASYURIDAE)

STEVE VAN DYCK

Van Dyck, S. 2002 5 31: Morphology-based revision of *Murexia* and *Antechinus* (Marsupialia: Dasyuridae). *Memoirs of the Queensland Museum* **48**(1): 239-330. Brisbane. ISSN 0079-8835.

The unremarkable, rat-like appearance of 16 named forms of small Irian Jayan and Papua New Guinean dasyurids previously assigned to *Antechinus* Waterhouse, 1837, and *Murexia* Tate & Archbold, 1937, has resulted in persistent taxonomic confusion. In this paper the two genera are systematically revised and a hypothesis of phylogenetic relationships proposed. I conclude that the New Guinea taxa assigned to *Antechinus* (pre-1984) represent three related but morphologically primitive taxa that lack clear signs of relationship to each other. They are referred to monotypic *Micromurexia* (for *M. habbema*), *Phascomurexia* (for *P. naso*), and *Murexechinus* (for *M. melanurus*) all but distantly related to Australian antechinusines. New Guinea *Murexia* is monotypic (*M. longicaudata*) and highly plesiomorphic. It has no especially close relationship with the more derived *rothschildi* which has traditionally been assigned to *Murexia* but is assigned here to *Paramurexia* gen. nov.; the Murexinae is not supported, and the Australian *Antechinus* forms a monophyletic group with *Phascogale*.

□ *Murexia*, *Antechinus*, Marsupialia, New Guinea, taxonomy.

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Two laconic remarks made by Schlegel (1866) in the original description of *Phascogale longicaudata*, had significance well beyond their immediate 19th century context ... 'Cette espèce rappelle, par sa taille, le jeune du rat ordinaire' [*This species calls to mind, by its build, the young of the common rat ...*], '... et offrant en général absolument les mêmes caractères que les *Antechinus* de l'Australie ...' [*... and offering in general absolutely the same characteristics as the Antechinus of Australia ...*].

Ever since Schlegel's time, the unremarkable, rat-like appearance of his *P. longicaudata* has consistently confounded its affinities with the suite of other equally unremarkable, rat-like dasyurids from New Guinea.

Schlegel's other observation that *P. longicaudata* shared attributes with the Australian *Antechinus* was later echoed by Thomas (1899) in his description of the Papua New Guinean species *Phascogale melanura*, '*P. melanurus* clearly belongs to the group comprising the small < *Antechini* > of Australia, *Ph. minima*, *flavipes* etc., and of which *Ph. longicaudata* is the largest member ...'.

Tate & Archbold (1941) assigned 3 New Guinean dasyurids *Phascogale tafa*, *P. melanurus* and a new species, *habbema* to the Australian *Antechinus* on the basis of their 'generalised forms'. In so doing Tate & Archbold

finally formalised the close link suggested by Schlegel & Thomas between the small dasyurids of Australia and those of Irian Jaya/Papua New Guinea.

Acceptance of the trans-Torresian distribution of *Antechinus* prevailed until 1984, when Woolley presented results of studies of phallic morphology in New Guinea dasyurids, indicating a very dubious relationship between Australian and New Guinean members of *Antechinus*, and thus challenging the integrity of the Phascogalinae (sensu Archer, 1982a) not long after consensus from a diversity of opinion indicated that *Antechinus* in Australia was not monophyletic (but included what we now regard as *Dasykaluta rosamondae*, *Pseudantechinus macdonnellensis*, *P. ningbing*, *Parantechinus apicalis* and *Pa. bilarni*). This was followed (Van Dyck, 1988) by a clarification of specific epithets applicable to '*Antechinus*' of New Guinea (*melanurus*, *habbema* and *naso*) but more importantly providing morphological confirmation that these species (and *Murexia*) deserved generic reclassification, that their inclusion in *Antechinus* was, as Woolley had suggested, inappropriate.

Kirsch et al. (1990), using DNA hybridisation, and Bayerstock et al. (1990), using albumin immunology, confirmed the closer relationship between New Guinea 'antechinusines' and New

Guinea *Murexia* than with Australian *Antechinus*. Krajewski et al. (1993) concluded that New Guinea *Antechinus* and *Murexia* formed a clade that was the sister-group of Australian antechinuses. Krajewski et al. (1994) called for the abolition of the Murexinae and Phascosoricinae, in favour of the Phascogalinae and the Dasyurinae (respectively). Krajewski et al. (1996), on the basis of analysis of cytochrome b sequencing, concluded that the Phascogalinae (sensu Archer, 1982a) actually consisted of 3 clades corresponding to *Phascogale*, Australian *Antechinus*, and New Guinean 'antechinuses' and *Murexia*. They also proposed monophyly of *Murexia* and all *Antechinus* apart from *Phascogale*, and recommended assignment of the New Guinea antechinuses *A. habbema*, *A. melanurus*, *A. naso* and *A. wilhelmina* (provisionally) to *Murexia*.

Since Schlegel's description of *P. longicaudata*, 15 species or subspecies of *Murexia* and *Antechinus* have been described from New Guinea. The primary objective of this study is to clarify the generic relationships of the New Guinea species previously assigned to *Antechinus*. At a specific level, there has been, since then, reasonable concurrence with other authors (Woolley, 1989; Krajewski et al., 1996), however, at the generic and subspecific levels there are major discrepancies between conclusions from morphological and molecular analyses.

Species assigned to *Antechinus* herein are: *A. stuartii* Macleay, 1841, *A. leo* Van Dyck, 1980, *A. subtropicus* Van Dyck & Crowther, 2000, *A. agilis* Dickman, Crowther & King, 1998, *Phascogale godmani* Thomas 1923, *Phascogale swainsonii* Waterhouse 1840, *Phascogale bella* Thomas 1904, *Phascogale flavipes* Waterhouse 1837, *Phascogale flavipes adusta* Thomas 1923, and *Dasyurus minimus* Geoffroy [Saint-Hilaire] 1803. *Antechinus habbema* Tate & Archbold, 1941 is assigned to *Micromurexia* gen. nov., *Phascogale naso* Jentink, 1911 is assigned to *Phascomurexia* gen. nov., *Phascogale melanura* Thomas, 1899 is assigned to *Murexechinus* gen. nov. and *Phascogale rothschildi* Tate, 1938 is assigned to *Paramurexia* gen. nov. *Murexia* now contains only *Phascogale longicaudata* Schlegel, 1866.

METHODS

Terminology of cranial morphology follows Archer (1976a), dental and external morphology follows Archer (1976b, 1981), and tooth number

follows Luckett (1993). Cranial and dental measurements were made with NSK electronic digital calipers (to 0.01mm). All specimens compared in diagnoses were adults with fully erupted $P^{3/3}$.

Specimens were examined from the Australian Museum, Sydney (AM M); Australian National Wildlife Collection, Division of Wildlife Research, Canberra (CM); Bernice Bishop Museum, Honolulu (BBM); Natural History Museum, London (BMNH); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); American Museum of Natural History, New York (AMNH); Museum National D'Histoire Naturelle, Paris (MNHN); Museo Civico Del Storia Naturale, Genova (MCSN); Museum of Comparative Zoology, Harvard College, Cambridge (MCZ); Zoologisches Museum der Humboldt-Universität zu Berlin (ZM); Queensland Museum, Brisbane (QMJ or JM).

I have examined type material of the species recognized herein (listed above) and species here placed in synonymy with them. Types of other *Antechinus* species not dealt with in the taxonomic section are: *Phascogale godmani* Thomas, 1923 (BMNH 1922.12.18.46), *Phascogale swainsonii* Waterhouse, 1840 (BMNH 60.1.5.18), *Phascogale swainsonii mimetes* Thomas, 1924 (BMNH 24.10.1.1), *Dasyurus minimus* Geoffroy, [Saint-Hilaire] 1803 (MNHN 1987-223), *Phascogale affinis* Gray, 1841 (BMNH 41.1241), *Phascogale (Antechinus) minimus maritima* Finlayson, 1958 (SAM M4985), *Phascogale bella* Thomas, 1904 (BMNH 4.1.3.102), *Phascogale flavipes* Waterhouse, 1837 (BMNH 1855.12.24.75), *Phascogale flavipes rufogaster* Gray, 1841 (BMNH 1841.1251), *Antechinus flavipes rubeculus* Van Dyck, 1982 (QM JM2676), *Phascogale leucogaster* Gray, 1841 (BMNH 1841.1244), *Phascogale flavipes adusta* Thomas, 1923 (BMNH 1922.12.18.54), *Antechinus stuartii* Macleay, 1841 (neotype AM M5294), *Antechinus subtropicus* Van Dyck & Crowther, 2000 (QM J17407), *Antechinus leo* Van Dyck, 1980 (QM J2372).

I present only the most economical primary synonymy. Species diagnoses attempt to describe absolute diagnostic features, while more relative diagnostic characters, appear in Remarks. In most instances subjective synonyms are dealt with in detail to provide reasonable justification for taxonomic decisions made here, and to remove subjectivity.

Pelage colours were compared with Ridgway (1912) and statistical significance between means was established through Students T-tests.

PHYLOGENETIC ANALYSIS

Binary coding of character states was rarely possible, and most characters were scored multistate. Both the branch and bound algorithm of Hennig '86 V1.5 (Farris, 1988) and PAUP version 4.0b2 (Swofford 1998) were used to analyse the data matrix in Table 8. A heuristic search of the data was completed using step-wise addition sequences, tree-bisection-reconnection (TBR) branch swapping, MULPARS, and zero branches collapsed to yield polytomies. The strict consensus (Bremer, 1990) of the most parsimonious trees was computed using PAUP and Hennig '86. Successive approximations character weighting (successive weighting) was implemented using PAUP with a base weight of 1000. Clados Version 1.2 (Nixon, 1992) was used to study character evolution. In the character matrix, *A. stuartii*, *A. agilis* and *A. subtropicus* are merged into the single taxon *Antechinus stuartii* for the analysis. In addition, a heuristic search of the data was invoked using 500 bootstrap pseudoreplicates, Branch-swapping, Tree-bisection-reconnection, MuTrees and a Consensus Tree formulated using the 50% majority-rule criterion (not shown).

TAXONOMIC HISTORY OF THE PHASCOGALINAE

Suprageneric classification within the Dasyuridae was reviewed and revised by Archer (1982a) and challenged by Westerman & Woolley (1993), and Krajewski et al. (1994, 1996). Goldfuss (1820) assigned Australian carnivorous marsupials to the tribe Dasyurini. From this tribe Waterhouse proposed the Dasyuridae and the Myrmecobiidae. Bonaparte (1838) removed *Thylacinus* from the Dasyuridae to the Thylacinidae, but proposed the Phascogalinae, within the Dasyuridae to, presumably, accommodate the smaller representatives. Gill (1872) erected a suborder, the Dasyuromorphia, to accommodate the Myrmecobiidae and the Dasyuridae (which contained subfamilies Sarcophilini, Dasyurinae and Phascogalinae). But Thomas (1888) did not adopt the Phascogalinae, and divided the Dasyuridae into the Myrmecobiinae and Dasyurinae. Iredale & Troughton (1934) (classifying only Australian mammals) recognised 3 subfamilies in the Dasyuridae:

Phascogalinae (*Antechinus*, *Planigale*, *Phascogale*, *Dasyercus*, *Dasyuroides*, *Sminthopsis* and *Antechinomys*), Dasyurinae and Thylacininae. Simpson (1945) assigned *Dasyurus*, *Dasyurops*, *Dasyurinus*, *Satanellus* and *Sarcophylus* to the Dasyurinae, which, along with the Phascogalinae, Myrmecobiinae and Thylacinidae accounted for the Polprotodontia. Tate (1947) instead, divided the Dasyuridae into the Dasyurinae (based on the reduction of P^3 , and I^2 being smaller than I^4) and the Phascogalinae to which he assigned *Antechinus*, *Murexia*, *Thylacinus*, *Sminthopsis*, *Antechinomys*, *Planigale* and *Phascogale*. Similarly, Laurie & Hill (1954) accommodated New Guinean representatives of *Murexia*, *Sminthopsis*, *Planigale* and *Antechinus* in the Phascogalinae. Ride (1964) recognised four marsupial orders, one of which, the Marsupicarnivora contained the superfamily Dasyuroidea made up of the Thylacinidae and Dasyuridae. The Dasyuridae contained Myrmecobiinae and the Dasyurinae (containing all dasyurid genera other than *Myrmecobius*). Kirsch (1977) used Gill's (1872) Dasyuromorphia to accommodate the Dasyuroidea which contained the Myrmecobiidae and the Dasyuridae.

POLYPHYLY OF THE PHASCOGALINAE. Several studies that suggested *Antechinus* was not monophyletic were based on phallic morphology (Woolley, 1982), interpretation of enzyme data (Baverstock et al., 1982) and cranial and dental examinations (Archer, 1982a; Kirsch & Archer, 1982). They specifically impacted on what we now regard as *Dasykaluta rosamondae*, *Pseudantechinus macdonnellensis*, *P. ninbing*, *Parantechinus apicalis* and *Pa. bilarni*. The broad spectrum of species, historically representing the Phascogalinae, was reduced by Archer (1982a), with restriction of its constituents to *Phascogale* and *Antechinus* (the New Guinea 'antechinuses', and 7 thin-tailed Australian antechinuses) on the putative synapomorphies of enlargement of I^1 , reduction in M^4 complexity, and slight reduction in posterior premolar size. At the same time Archer erected the Murexinae, for *Murexia longicaudata* and *M. rothschildi*, in recognition of the primitive nature of the dentition and basicranium.

Woolley's (1984) studies of phallic morphology in New Guinea dasyurids indicated a more than dubious relationship between Australian and New Guinean members of *Antechinus*, again challenging integrity of the Phascogalinae. This was followed (Van Dyck, 1988) by a clarification

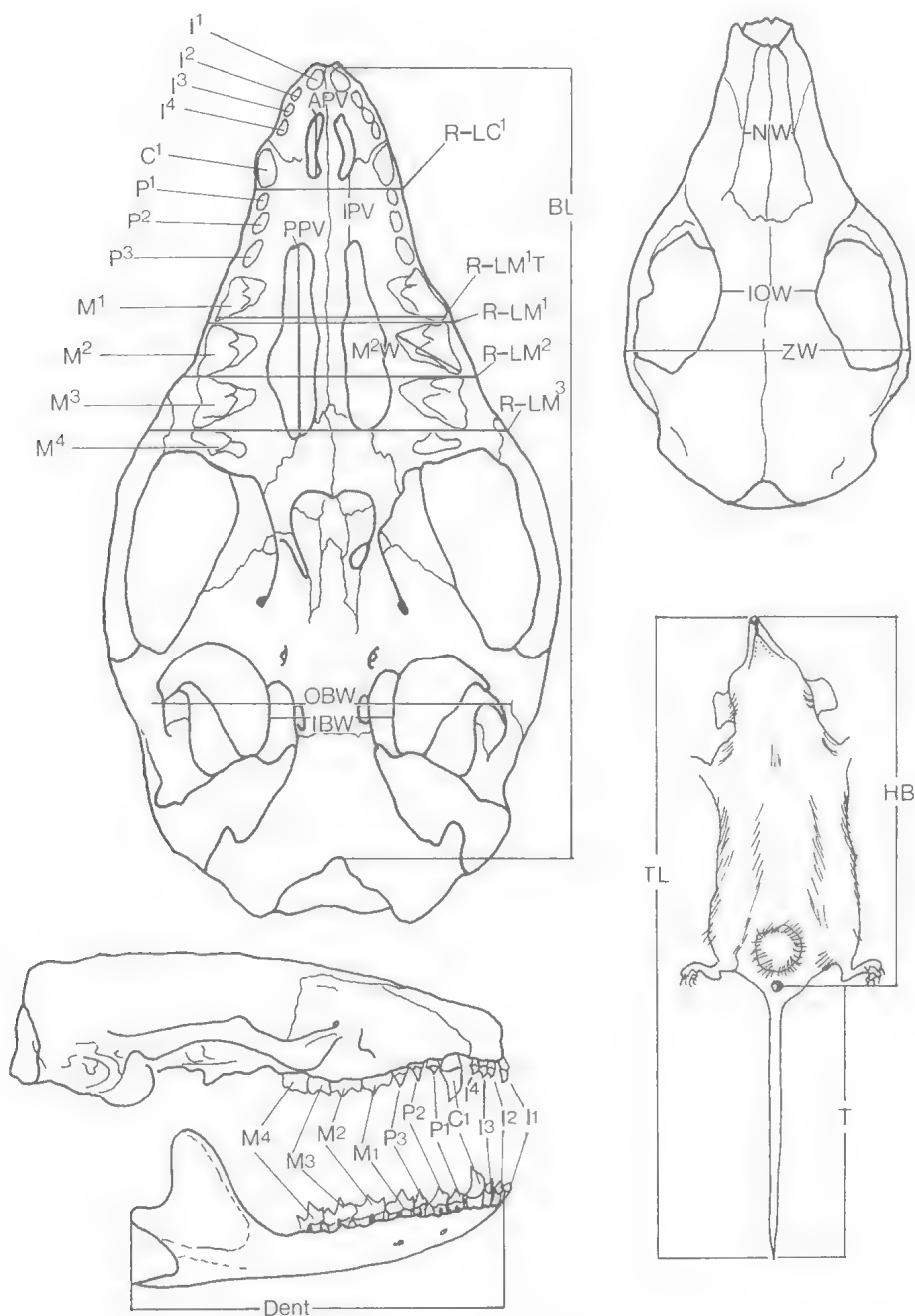


FIG. 1. Tooth numbering and limits of measured dimensions. Abbreviations are: APV = anterior palatal vacuity length; BL = basicranial length; Dent = dentary length; HB = head and body length; IBW = distance between right and left auditory bullae; IOW = interorbital width; IPV = inter-palatal vacuity length; M^2W = width of second upper molar; NW = nasal width the level of the premaxillary/nasal/maxillary junction; OBW = basicranial width from outside right and left auditory bullae; PPV = posterior palatal vacuity length; R-LC¹ = rostral width at the level of the upper canines; R-LM¹ = rostral width at the level of the first upper molars; R-LM¹T = width between the ectolophs of right and left first upper molars; R-LM² = rostral width at the level of the second upper molars; R-LM³ = rostral width at the level of the third upper molars; T = tail length; TL = total length, body and tail; ZW = zygomatic width.

of specific epithets applicable to the 'Antechinus' of New Guinea (*melanurus*, *habbema* and *naso*) but more importantly providing morphological confirmation that these species deserved generic reclassification, that their inclusion in *Antechinus* was inappropriate. The specific epithets were tentatively confirmed by Woolley (1989), who again drew attention to distinction between Australian and New Guinean 'antechinuses'. Kirsch et al. (1990), using DNA hybridisation, and Baverstock et al. (1990), using albumin immunology, confirmed the closer relationship between small New Guinean 'antechinuses' and New Guinean *Murexia* than with Australian *Antechinus*. While both studies concluded, however, that New Guinean 'antechinuses' were monophyletic with *Murexia*, Baverstock et al. (1990) concluded that Australian species of *Antechinus* and *Phascogale* formed a monophyletic group (also see Aplin et al., 1993), while Kirsch et al. (1990) found *Phascogale* to be part of a broader context i.e., the sister group of all Australian and New Guinean *Antechinus* and *Murexia*. Kirsch's results (with respect to *Phascogale*) were confirmed by Krajewski et al. (1993) who also concluded that New Guinea species of *Antechinus* and *Murexia* formed a clade that was the sister-group of Australian antechinuses. On the basis of cytochrome-*b* and MC'F data, however, Westerman & Woolley (1993) suggested *Murexia longicaudata* and *M. rothschildi* were allied to the Dasyurinae, not the Murexinae.

Krajewski et al. (1994) called for abolition of Muricinae (sic) and Phascolosoricinae, in favour of Phascogalinae and Dasyurinae respectively. Krajewski et al. (1996) presented the following results of phylogenetic analysis of cytochrome *b* sequences from 10 species of the Phascogalinae: the subfamily consisted of 3 clades corresponding to 1. *Phascogale* 2. Australian *Antechinus*, and New Guinean 'antechinuses' and 3. *Murexia*. There was monophyly of *Murexia* and all *Antechinus* apart from *Phascogale*; a sister-species relationships existed between *A. melanurus* and *A. naso*, and between *A. stuartii* and *A. swainsonii*. They also suggested early divergence of *A. habbema*. But finally, and most importantly, Krajewski et al. recommended assignment of the New Guinea antechinuses *A. habbema*, *A. melanurus*, *A. naso* and *A. wilhelmina* (provisionally) to *Murexia*. This was echoed by Armstrong et al. (1998).

Morphological comparisons presented here suggest that *M. habbema*, *M. longicaudata*, *P.*

naso, *P. rothschildi* and *M. melanurus* represent a suite of related but morphologically primitive taxa that lack clear signs of close relationship but that have minor autapomorphies to distinguish them from one another. They are largely plesiomorphic in their teeth and skulls relative to Australian *Antechinus* and other dasyurid genera.

SYSTEMATICS

Family DASYURIDAE

Antechinus Macleay, 1841

Dasyurus (in part) Geoffroy [Saint-Hilaire] 1803.

Phascogale (in part) Temminck 1824.

Phascogale (in part) Thomas 1888.

TYPE SPECIES. *Antechinus stuartii* Macleay, 1841. Based on a drawing and written description by J. Stuart. Neotype AM M5294, adult ♂ in ethanol and skull from Waterfall [Royal] National Park, New South Wales.

SPECIES INCLUDED. *godmani* (Thomas, 1923); *swainsonii* (Waterhouse, 1840); *minimus* (Geoffroy [Saint-Hilaire], 1803); *bellus* (Thomas, 1904); *flavipes* (Waterhouse, 1837); *adustus* (Thomas, 1923); *subtropicus* Van Dyck & Crowther, 2000; *leo* Van Dyck, 1980, *agilis* Dickman et al., 1998.

GENERIC DIAGNOSIS. Penis with a bifid tip. Tail shorter than the head-body length (the tail does not possess a terminal brush or ventral crest as in *Phascogale*, *Dasyuroides*, *Dasyercus*, *Antechinomys*, *Sminthopsis longicaudata*). Pelage not including dorsal striping (as in *Paramurexia*, *Myoictis*, *Phascolosorex*, *Thylacinus*) or spots (as in *Dasyurus*). M¹ of reduced protocone breadth, with complete or incomplete anterior cingulum but with the anterior margin indented posteriorly, and never anteriorly convex (as in *Micromurexia*, *Murexia*, *Phascomurexia*, *Paramurexia*, *Murexechinus*, *Myoictis*). P³ might be relatively reduced, never reduced to a spicule or lost from the premolar row (as in *Dasyurus*, *Sarcophilus*, *Dasykaluta*, *Parantechinus*, *Dasyuroides*, some *Planigale*). M¹ with reduced paraconid but never greatly reduced as in *Parantechinus*, *Pseudantechinus*, *Dasyurus*, *Sarcophilus*). Tail not incrassate (as in some *Sminthopsis*, *Pseudantechinus*, *Dasykaluta*, *Dasyercus*). Auditory bullae not enormously enlarged (as in *Ningui*, *Dasykaluta*, *Pseudantechinus*, *Dasyuroides*, *Phascogale*, some *Sminthopsis*). Squamosal and frontal bones not in contact (as in *Sminthopsis*, *Thylacinus*, *Neophascogale*, *Phascolosorex*, *Planigale ingrami*, *Myoictis*, *Antechinomys*). Metacristids and hypocristids not transverse to the long axis of the skull (as in *Sminthopsis*, *Thylacinus*,

Ningau). Skull non-dolichocephalic (unlike *Planigale*). Striated foot pads. Rudimentary pouch. Post-mating mortality of males.

DESCRIPTION. *Dentition.* Upper Incisors: I^1 is not needle-like, taller-crowned than other incisors and may be very procumbent in some species (*adustus*) or totally non-procumbent in others (*minimus*). Right and left I^1 may be separated by a small gap (*leo*) or may touch (most others), however in *swainsonii* and *minimus* R and $L I^1$ form a V-shaped cutting wedge. I^1 crown may be narrow, long, pointed and curved, the arc of this curve orienting along the incisor row (*godmani*) or almost lensate, triangular, uncurved and flaring (*swainsonii*, *minimus*), alternatively, it may be massive, strongly curved, and almost caniniform (*adustus*). In most species it is separated from I^2 by a distinct diastema (however, in *swainsonii* and *minimus* it is not). I^{2-4} may be relatively compressed laterally (lensate) with broad roots (*swainsonii*) or narrowly rooted with heavier, more massive crowns (*bellus*, *leo*). I^{2-4} are invariably cingulated, this may be relatively weakly defined leading to a lack of differentiation between wide roots and crowns (*godmani*, *minimus*, *swainsonii*) or heavy (*adustus*). Relative crown size in I^{2-4} varies from overall approximate equality (*swainsonii*, *minimus*, *godmani*) to a condition of decreasing size, $I^2 > I^3 > I^4$ (*leo*, *flavipes*, *adustus*, *stuartii*, *agilis*, *subtropicus*). I^1 lacks a secondary posterior cusp. It is also characterised by an increased crown height and a narrow root. In overall crown size $I^2 > I^3 > I^4$. Only in *adustus* is I^4 conspicuously enlarged but not to the extent seen in *P. calura* and *P. tapoatafa*.

Upper Canines: May be relatively long (not as long as in *Micromurexia*, *Murexia*, *Phascomurexia*), curved, needle-like and weakly cingulated (*godmani*, *swainsonii*, *minimus*) or more robust as in *leo*. There is no anterior cusp but a very small posterior cingular cusp is sometimes present (*leo*, *flavipes*, *adustus*, *stuartii*, *agilis*, *subtropicus*, *swainsonii*).

Upper Premolar: Rows may be long with the premolars widely spaced and exceptionally slender (*swainsonii*, *minimus*), or alternatively, the teeth may be crushed and bulbous (*leo*, *flavipes*, *adustus*). Posterior cusps on P^3 may be seen in *swainsonii*, *minimus* and *godmani*. In all species $P^3 > P^2 > P^1$ and in none is P^3 lost.

Upper Molars: The anterior cingulum on M^1 originates in a small but prominent stylar cusp A, and, in species where the cingulum is broad and

complete, continues into the trigon basin (*adustus*, *stuartii*, *agilis*, *subtropicus*, *swainsonii*). In those species where the cingulum is narrow and almost incomplete, it becomes indistinct at the base of the paracone apex (*bellus*, *leo*, *flavipes*). The anterior margin of M^1 is indented posteriorly, and never anteriorly convex (as in *Micromurexia*, *Murexia*, *Phascomurexia*, *Paramurexia*, *Murexechinus*, *Myoictis*). M^2 is invariably longer than M^3 in which the ectoloph is indented to the greatest extent in *bellus*, *leo* and *flavipes*. Stylar cusp B lies at the termination of the anterobuccally oriented preparacrista. It is more reduced than in *Micromurexia*, *Murexia*, *Phascomurexia*, *Paramurexia*, *Murexechinus* and *Myoictis*, but it is never reduced to a minute spur or entirely lost. The paracone of M^1 is approximately half the height of the metacone, it is never fused with stylar cusp B. Stylar cusp D of M^1 and M^2 is usually taller and more prominently conical than in *Micromurexia*, *Murexia*, *Phascomurexia*, *Paramurexia*, *Murexechinus* and *Myoictis* and reaches its greatest development for the genus in *swainsonii*. The condition in *godmani* most closely approximates that reduced condition in New Guinea taxa mentioned above. Stylar cusps C and E are usually not prominent and a posterior cingulum is usually absent in *bellus*, *leo*, *minimus* and *godmani*. M^4 protocone is variably reduced but minute in *bellus* and *leo*, slightly larger in *adustus*, *minimus*, *stuartii*, *agilis*, *subtropicus* and *godmani*, and largest in *swainsonii*.

In M^2 and M^3 , the broad anterior cingulum which contacts the metastylar corner of M^1 tapers very quickly as it progresses along the base of the paracrista and usually degenerates labially, well buccal to the base of the paracone apex (in *A. adustus* the anterior cingulum is usually just complete). No protoconule is visible. M^2 lacks stylar cusps A, C and E. Stylar cusp D is slightly reduced in M^2 to a very small, sharp peak.

In M^4 the broad anterior cingulum usually terminates quickly away from metastylar corner of M^3 , however a continuous anterior cingulum is often present in *adustus*, *stuartii*, *agilis*, *subtropicus* and *flavipes*. A posterior cingulum is absent. M^4 shows some metacone development in *leo*, *swainsonii*, *minimus* and *godmani* but generally the metacone is greatly reduced.

Lower Incisors: I_1 crown is invariably larger than I_2 which is subequal to I_3 except in *swainsonii* in which $I_1 > I_2 > I_3$. Lower incisors are oval in anterolateral view and gouge-like in occlusal view. I_1 and I_2 are almost prostrate in *flavipes*,

slightly more erect in *bellus*, *leo*, *adustus*, *minimus* and *godmani*, and most erect in *adustus* and *swainsonii*. I_3 is usually incisiform except in *minimus* where it is premolariform in lateral view with a large posterior cusp. The lower canine rests against this cusp. In occlusal view a small notch separates the posterior cusp from a prominent posterolingual lobe which wraps posteriorly around the canine and the crown enamel of primary and posterior cusps folds noticeably so that the crest of the two cusps bisects the tooth longitudinally. In some species the heel is narrower on I_3 than I_1 (*bellus* in particular).

Lower Canines: C_1 may be caniniform and strongly sickle-shaped (*godmani*, *minimus*) or thicker and more erect (*leo*, *adustus*, *flavipes*, *stuartii*, *agilis*, *subtropicus*). In *swainsonii* however, C_1 is premolariform with minimal curvature from root to crown. The canine may be weakly cingulated buccally and lingually (*bellus*, *godmani*, *swainsonii*, *agilis*, *subtropicus*, *stuartii*). *A. leo* has weak buccal cingula but is strongly cingulated lingually, while strong buccal and lingual cingula are found in *minimus* and *adustus*.

Lower Premolar: Rows may be long, with the premolars widely spaced and exceptionally slender (*swainsonii*, slightly less so in *minimus* and *godmani*), or alternatively, the teeth may be more crushed and bulbous (*leo*, *bellus*, *flavipes*, *adustus*) and in these the P_3 is often oriented more transversely in the tooth row. Lower premolars are cingulated. Postero-lingual lobing occurs in *bellus*, *leo* and *flavipes*. P_3 is never absent. The bulk of each premolar mass is concentrated anteriorly to the line drawn transversely through the middle of the two premolar roots.

Lower Molars: M_1 talonid is wider than the trigonid and the anterior cingulum is present but usually poorly developed or absent (variably absent in *stuartii* and *swainsonii*). If the cingulum is present it terminates at the posterior base of the protoconid. There is a very weak buccal cingulum in most species but again, it is not always present in *stuartii* and *swainsonii*. It is confined between the bases of the protoconid and hypoconid as a thickened bulge of enamel. The paraconid which is more reduced than in *Micromurexia*, *Murexia* and *Phascomurexia* but similar to that seen in *Paramurexia* and *Murexechinus*, appears in occlusal view as a small steeply-sided or low spur, the lingual edge of which makes an appreciable swelling on the

endoloph of M_1 in *bellus*, *godmani*, *minimus* but little or no contribution in *leo*, *swainsonii*, *adustus*, *agilis*, *subtropicus*, *flavipes* or *stuartii*. The metaacristids are roughly oblique to the long axis of the dentary. The cristid obliqua extends from the hypoconid to the posterior wall of the trigonid, intersecting the trigonid at a point directly below the tip of the protoconid in *bellus*, *leo*, *godmani*, but slightly lingual to that in the other species (*stuartii* sometimes slightly buccal). From the base of the metaconid posteriorly, the talonid endoloph may follow the line of the dentary past the base of the entoconid and along the dentary line to the hypoconulid as in *leo*, *swainsonii*, *minimus*, *adustus* or it may take a sharp lingual orientation until it meets the base of the entoconid where it then orients buccally to meet the hypoconulid (*bellus*, *godmani*, *stuartii*). In M_1 the entoconid is usually minute or low.

In M_2 the talonid is usually wider than that of the trigonid. The anterior cingulum is poorly developed in all species and terminates lingually to accommodate the hypoconulid notch and continues very weakly into the buccal cingulum which terminates slightly anterior to a vertical line drawn through the tip of the hypoconid. Buccal cingula are strongly present only in *A. leo*, and posterior cingula in *leo*, *bellus*, *swainsonii* and *adustus*. The paraconid is well-developed throughout but is the smallest trigonid cusp. It is slightly taller than the entoconid which is well developed in *godmani*, *swainsonii*, variably in *stuartii* and weakly developed in the rest. Its greatest reduction is seen in *bellus*, *leo* and *flavipes*. The hypoconid is shorter than the entoconid. The metaacristid is more steeply inclined from the protoconid to the metaacristid fissure than from the entoconid to the metaacristid fissure. The cristid obliqua extends to the base of the protoconid, intersecting the trigonid at a point directly below the protoconid tip, but well buccal to the metaacristid fissure. From the base of the entoconid posteriorly, the talonid endoloph follows the line of the dentary axis in *leo*, *godmani*, *swainsonii*, *minimus* and *adustus*, but takes a more lingual orientation in *bellus* and *stuartii*, and a more buccal orientation in *flavipes*.

In M_4 of most species the talonid is slightly wider than the trigonid. The anterior cingulum is poorly developed in all but *leo* and *adustus* and buccal and posterior cingula are weak in all but *leo* and *bellus*. The cristid obliqua intersects the trigonid at a point more buccal to the longitudinal vertical mid-line through the protoconid tip than

in M_2 . This intersection does not, however, reach the point directly below the metacristid fissure. The endoloph of the talonid in M_3 orients directly along the line of the dentary in *bellus*, *godmani*, *adustus* but takes a more buccal orientation in *leo*, *swainsonii*, *minimus*, *flavipes* and variably in *stuartii*. The entoconid is relatively tall only in *minimus*, *godmani*, *adustus* and variably in *stuartii*, *agilis* and *subtropicus*.

The M_1 trigonid is wider than the talonid. The anterior buccal and posterior cingula are as in M_2 and M_3 . The paraconid is shorter than the metaconid. Talonid cusps are reduced to 2 in *bellus*, *adustus*, *stuartii*, *agilis*, *subtropicus*, *swainsonii*, *minimus* and *godmani* and 1 in *leo* and *flavipes*. The hypoconid is reduced relative to M_3 . The cristid obliqua is a high crest which intersects the trigonid directly below the metacristid fissure, this being markedly more lingual than intersections of the cristid obliqua for M_1 - M_3 .

Skull, Externals, etc. The skulls of *swainsonii*, *minimus* and *godmani* are the most elongate (skull width across lachrymals: length l^1 to lachrymal canal 76-84%), followed by *leo*, *flavipes*, *stuartii*, *agilis*, *subtropicus* (85-93%) and the broadest rostrum is found in *bellus* and *adustus* (94-102%). Nasal fluting is rarely found, but the condition is sometimes suggested in *leo*. The tympanic wing of the alisphenoid is generally poorly developed in all except *bellus* where there is moderately greater expansion. The pars mastoidea and adjacent squamosal are poorly expanded in all species and only in *bellus* is the skull 'Roman nosed'. It is slightly domed in *swainsonii* and *minimus*. Squamosal/frontal contact does not occur in any species, nor do palatine vacuities. Anterior palatal vacuities are very large in *swainsonii*, *minimus* and smallest in *bellus*. Posterior palatal vacuities are largest in *swainsonii* and *subtropicus*. Only in *bellus*, *leo* and *godmani* is the supratragus folded. The tail is shorter than the head-body length, but it is further reduced in *swainsonii* and *minimus*. All hind foot pads are striated and very long claws are found in *swainsonii* and *minimus*. All species lack body stripes and all females possess a rudimentary (ephemeral) pouch in which nipple number may vary from 6 (*godmani*, *adustus*) to 10 (*leo*, *bellus*) to variable (all others). All males die soon after mating.

REMARKS. The analysis that follows suggests that *Phascogale* is monophyletic with *Antechinus*, and represents antechinuses in their

most derived state. This is supported by albumin immunology assessment (Baverstock et al., 1990; Aplin et al., 1993) but not through cytochrome b sequence analysis (Krajewski et al., 1993, 1996). Until some consensus is reached between the biochemical and morphological schools on this and broader New Guinea issues discussed later, I am reluctant to propose that *Phascogale* should accommodate all Phascogalines (sensu Archer, 1982a) or that *Antechinus*, revert to subgeneric status to accommodate all antechinuses.

Micromurexia gen. nov.

Antechinus (in part) Macleay, 1841.

TYPE AND ONLY SPECIES. *Antechinus habbema* Tate & Archbold, 1941: 8), based on AMNH 109812, adult ♂ puppet skin with skull extracted, from 9km NE of Lake Habbema, N slope of Mt Wilhelmina, Irian Jaya, 4°05'S, 138°50'E, at 2,800m.

GENERIC DIAGNOSIS. M^1 very broad, with wide protocone and complete anterior cingulum, the anterior margin of this tooth is straight or anteriorly convex, but never indented or concave. Talonid on M_1 relatively unreduced, retaining an entoconid, hypoconid and hypoconulid. Tail longer than the head-body length.

It is distinguished from *Phascosorex* and *Myoictis* by its lack of dorsal body stripes, and from *Neophascogale* by lacking a white tail-tip.

Micromurexia is separable from *Phascomurexia* by the absolutely shorter length of its upper and lower molar rows.

Micromurexia differs from *Murexechinus* by: ears lack post-auricular patches and pelage more uniform shade throughout rather than rufous post-auricular patches and definite warming of tones toward rump; claws slightly curved and slender rather than strongly curved and thick; tail dorso-ventrally bicoloured rather than uniform black (sometimes uniform dark brown); I^1 narrow, needle-like and minutely crowned rather than broad, claw-like and heavily crowned; I^{2-4} uncungulated, narrow and with minimal curvature of the crown rather than strongly cingulated buccally and lingually, blade-like and robust; C^1 extremely long and slender rather than short and thick; premolars uncrowded and narrow with P^1 separate from P^2 rather than premolars crowded, wide and robust; lower molars with greatly developed entoconids (e.g., M_3 entoconid taller than paraconid in *Mi. habbema*) rather than lack of development in *Mu.*

melanurus (where in M3 entoconid is shorter than paraconid); nasals raised and fluted.

Micromurexia is separable from *Murexia* by its smaller values for the following measurements (the ranges (R) associated with each measurement do not overlap (Tables 1, 4)); BL₁, ZW, OBW, IBW, R-LC¹, R-LM¹, R-LM², R-LM³, R-LM¹T, I¹-M¹, P¹⁻⁴, M¹⁻⁴, M²W, I₁-M₁, P₁₋₄, M₁₋₄, M₂W, TL and HF.

Micromurexia is separable from *Paramurexia* by its smaller values for the following measurements (ranges (R) associated with each measurement do not overlap (Tables 1, 5)); BL₁, ZW, OBW, IBW, R-LC¹, R-LM¹, R-LM², R-LM³, R-LM¹T, I¹-M¹, M¹⁻⁴, M²W, I₁-M₁, P₁₋₄, M₁₋₄, M₂W. It lacks a black, dorsal body stripe.

Micromurexia habbema

(Tate & Archbold, 1941)

(Figs 2, 3, 6, 7)

Antechinus habbema Tate & Archbold, 1941: 3

Antechinus hageni Linsley, 1952: 29n

HOLOTYPE. American Museum of Natural History, AMNH 109812, Adult male puppet skin with skull extracted (both skin and skull in excellent condition, but teeth badly worn).

TYPE LOCALITY. 9km NE of Lake Habbema, north slope of Mt Wilhelmia, Irian Jaya, 4°05'S, 138°50'E at 2,800m

COLLECTOR. W.B. Richardson, 21 October 1938.

DIAGNOSIS. As for genus.

DESCRIPTION. Holotype AMNH 109812. *Pelage* (Fig. 2). Fur of the mid-back (7.7mm long) with the basal 6.4mm Slate Color, median 1mm Clay Color and apical 0.3mm black (Fuscous). The back appears overall to be Sepia. Medially thickened Fuscous spines (guard hairs) are interspersed through the fur and are up to 12mm long on the rump (basal 7.5mm Slate, median 2.5 Fuscous, apical 2mm colourless) and reduce to 2mm where they terminate between the eyes on the crown of the head. Fur on and below the shoulders, thighs flanks and chin lacks black (Fuscous) tips on guard hairs and these areas and belly appear Cream Buff to Chamois. The harshness of the guard hairs is reduced from rump to crown by the apical 2mm being colourless this giving a warmer tone to the fur colour compared to specimens from Mt Wilhelm. At the anterior corner of each eye a small patch of dark hairs sweeps to midway along the top and bottom eyelid thereby creating a half eye-ring. The remainder of fur around the eye is an

orange-brown (Sepia). A warm patch of Clay Color hairs is found anterior to each pinna. The soft ventral fur (8mm long on the belly) is Dark Neutral Gray on the basal 6mm and Pale Cinnamon-Pink on the apical 2mm and is interspersed with Cream-Buff medially thickened guard hairs 10mm long. The belly is thus an overall patchy Greyish Olive. Forefeet are very thinly covered with Hair Brown (greyish-brown) hairs. Hindfeet are more thickly covered with a mixture of white and Hair Brown hairs, giving the feet a peppered appearance. The tail (Figs 6, 7) is weakly bicoloured with short dorsal hairs averaging 2mm along its length and increasing to 4mm at its tip. These dorsal hairs are a uniform Saccardo's Umber. Hairs on the ventral surface are longer, averaging 5mm along its length increasing to 7mm at the tip. (This ventral 'crest' has been screwed around to the right hand side during preparation of the puppet skin). These ventral hairs are also uniform Saccardo's Umber.

Vibrissae. Approximately 17 mystacial vibrissae occur on each side and are up to 18mm long. The more dorsal mystacial vibrissae are coloured Fuscous Black while those lower are colourless: supra-orbital vibrissae (Fuscous Black becoming clear) number 1 left and 2 right; genals (Fuscous Black and colourless) number 8 left and 7 right; ulna-carpals (colourless) number 4 right and 5 left; submentals (colourless) number 4.

Tail (Figs 6, 7). The tail is much longer than the head and body length but in the holotype the tip of the tail has been broken off. It is thin and tapers toward the tip.

Hindfoot. Long hallucal and post-hallucal pads are narrow and fused. Apical granules are fleshy, enlarged, elongate and striate. There is an auxiliary apical granule outside and adjacent to the first interdigital pad. No other auxiliary granules are visible.

Ears. Pinnae large, with complex supratragus, posterior margin thickened, distal end reflected ventrally, reflected tip slightly concave.

Dentition (Fig. 3). Upper Incisors: I¹ is narrow and needle-like, slightly procumbent and heavily worn on the crowns, taller crowned than all upper incisors and separated by a small diastema from I². Left and right I¹ are widely separated and the crowns appear to be directed away from each other. Crown height for I²⁻⁴ is difficult to judge as all are badly and irregularly worn. I¹ appears to be greater in crown height than I³ which appears to be greater than I². All upper incisors are badly worn but appear to lack buccal and lingual

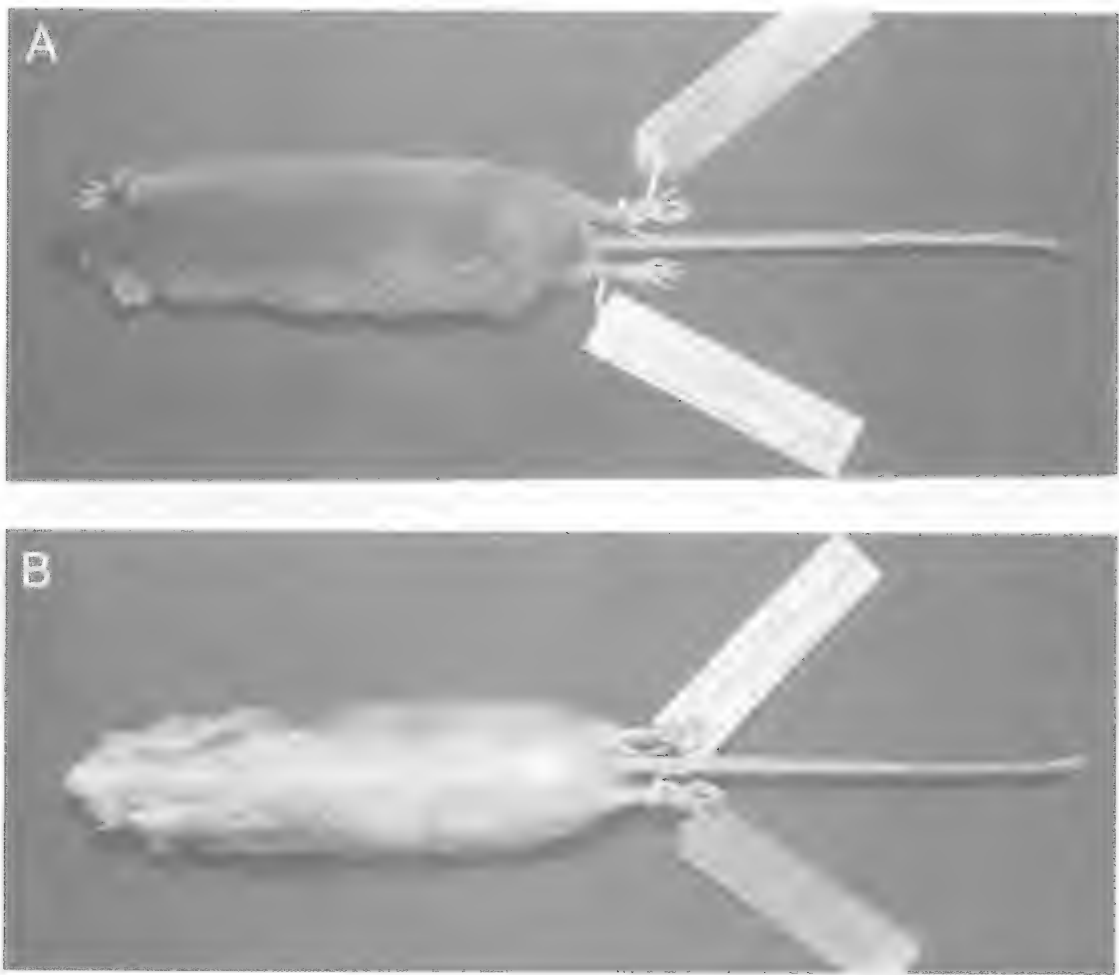


FIG. 2. Holotype of *Antechinus habbema* Tate & Archbold, 1941 (now *Micromurexia habbema*). AMNH 109812, study skin; A, dorsal view; B, ventral view. TL = 252mm; HB = 112mm; TV = 140mm; HF = 21mm; E = 13mm.

cingula. I^4 carries no anterior or posterior cusp, although excessive wear may have eliminated these. Roots of I^4 are wide.

Upper Canines: C^1 is slender and caniniform with no appreciable boundary between root and crown. There are no buccal or lingual cingula. R and L C^1 are abnormally worn with thegotic wear anteriorly and posteriorly over the tip. Posterior notching occurs at the root level. The thegotic wear appears to have been caused by poorly occluding R and L C_1 .

Upper Premolars: The premolar row is long, narrow and characterized by the separation of P^1 from P^2 and P^3 . There is a diastema between C^1 and P^1 , but LP^2 touches LP^3 ; RP^2 is separated from RP^3 . P^1 and P^2 carry strong buccal and weak lingual cingula but P^3 lacks a lingual cingulum

and its buccal cingulum is weak. P^1 crown is shorter than P^2 crown which is shorter than P^3 . P^3 has a massive posterior root. There are small but clearly definable anterior cingular cusps on P^1 and P^2 . No posterior cusps are visible although the poorly occluding lower jaw has caused excessive, abnormal wear to P^1 resulting in its posterior half having been worn away.

Upper Molars: All upper molars are excessively worn. The posterior tip of P^3 lies in the parastylar corner of M^1 . In M^1 stylar cusp A is worn away. The anterior cingulum below stylar cusp B is so badly worn that it is impossible to tell if it is complete. Stylar cusp B and the M^1 paracone are worn off and there is no protoconule present. Stylar cusp C is not visible on either L or R M^1 and stylar cusp E is not visible. M^1 has a weak

posterior cingulum. The RM^1 metacone is worn off to be coplanar with the trigon basin. Styler cusp D is worn away.

In M^2 the paracone is worn almost away and the anterior cingulum is difficult to detect, however it seems narrow, contacting the metastylar corner of M^1 and tapering quickly down to the base of the protocone apex. There is no visible protoconule. M^2 lacks styler cusps A, C and E. Styler cusp D is very high but this is probably an artefact of the metacone's wearing away. There is a weak posterior cingulum on LM^2 . RM^2 is worn down to the level of the posterior cingulum.

In M^3 the anterior cingulum is worn but is probably narrowly present. There is slight evidence of an anterior cingulum at the base of the paracone. Styler cusp D is reduced to a very small blunt peak. Styler cusps C and E are absent.

In M^4 the anterior cingulum appears complete. The paracone is greatly worn and a posterior cingulum is absent. The protocone is reduced and narrow. A small crest analogous to the metacone is present. In occlusal view the angle between postprotocrista and premetacrista is close to 80° .

Lower Incisors: I_1 is taller in crown height than I_2 . I_1 and I_2 are oval in anterolateral view and gouge-like in occlusal view. I_2 is slightly taller in crown height than I_3 . I_3 is small, premolariform in lateral view with an inconspicuous posterior cusp at the base of the crest which descends posteriorly from the apex of the primary cusp. The lower canine rests against this posterior cusp. In occlusal view, a small notch separates the posterior cusp from the prominent posterolingual lobe, and crown enamel of the primary and posterior cusp folds slightly lingually such that the longitudinal crest of the 2 cusps bisects the tooth, with 1/3 of enamel buccal to the crest and 2/3 lingual.

Lower Canines: C_1 is slender and caniniform, with erect projection and slight curvature from root to crown tip. It has weak buccal and lingual cingulation and no posterior cusp. Both R and L C_1 sustain appalling, abnormal thegotic wear in the form of deep posterior cuts where the ill-occluding C^l has stabbed into the posterior half of the lower canine.

Lower Premolars: P_{1-3} are unevenly spaced with RP_1 almost touching RP_2 which almost touches RP_3 . LP_1 is widely separated from LP_2 which nearly touches LP_3 . They are weakly cingulated buccally and lingually. In crown height P_2 is taller than P_3 which is taller than P_1 . All premolars are narrow. All possess posterior cusps. P_1 possesses a minute anterior cusp. The bulk of each premolar

mass is concentrated posteriorly to a line drawn transversely through the middle of the two premolar roots. Postero-lingual lobes are not a feature of the slender lower premolars.

Lower Molars: All lower molars are worn, they are narrow and lie in a relatively short premolar row. The M_1 talonid is much wider than the trigonid and the anterior cingulum is poorly developed. It originates at the anterior base of the paraconid and terminates at the anterior base of the protoconid. There is a very weak buccal cingulum. The well-developed paraconid appears in occlusal view as a small oblique spur, the lingual edge of which makes no appreciable swelling on the endoloph of M_1 . In lateral view the paracristid is almost 45° to the horizontal from the paraconid to the paracristid fissure, and 25° from the paracristid fissure to the protoconid (measured from the vertical, posteriorly). The metacristid is slightly oblique to the long axis of the dentary while the hypocristid is transverse. The protoconid and paraconid are worn, and the talonid basin eroded so badly that the cristid obliqua is short and extends from the hypoconid to the posterior wall of the trigonid intersecting the trigonid slightly lingual to that point probably directly below the worn-off tip of the protoconid.

The hypocristid terminates midway between the hypoconulid without veering toward the very tall, broad entoconid. From the base of the metaconid posteriorly, the talonid endoloph takes a very sharp lingual orientation then swings back buccally, posterior to the entoconid, until the base of the hypoconulid.

In M_2 the talonid is wider than the trigonid. The anterior cingulum is poorly developed originating lingually at a very weak and worn parastylid notch against which the M_1 hypoconulid is abutted. There is no buccal cingulum. A narrow, weak posterior cingulum extends from the hypoconulid to the posterior base of the hypoconid. The paraconid is badly worn and is the smallest trigonid cusp (even the entoconid is taller). The entoconid is tall and there is no metastylid present. The cristid obliqua extends from the hypoconid to the posterior wall of the trigonid intersecting the trigonid at a point which cannot be assessed from the badly worn protoconid and metaconid. The hypocristid extends from slightly anterior and buccal to the hypoconulid to the tip of the hypoconid. From the base of the metaconid posteriorly, the endoloph bulges out lingually around the entoconid swelling, and buccally to the hypoconulid tip.

In M_1 the trigonid is narrower than the talonid. A small parastylid wraps around the hypoconulid of M_2 and there is a weak anterior cingulum on M_3 . The posterior cingulum is as in M_2 . The cristid obliqua intersects the trigonid at a point well lingual to the longitudinal vertical midline drawn through the tip of the protoconid, and directly below the metaacristid fissure. The entoconid is very tall. The endoloph takes a more buccal orientation than that seen in M_2 so that only a swelling of entoconid is seen in occlusal view. The rest of M_3 morphology is as in M_2 .

In M_4 the trigonid is wider than the talonid. The anterior cingulum is as in M_2 but more poorly developed and a posterior cingulum is absent. Of the 3 main trigonid cusps the metaconid is slightly taller than the paraconid, but both are dwarfed by the protoconid. The hypoconid of M_4 is small in comparison to that on M_3 . Between the hypoconid and the base of the metaacristid the cristid obliqua forms a low, worn crest which contacts the trigonid wall below the metaacristid fissure. There is no reduction of talonid crown enamel below the cristid obliqua so the talonid appears (in occlusal view) as a wide shelf extending from the trigonid wall. The entoconid is prominent as are the hypoconulid and hypoconid.

Skull (Fig. 3). The skull of *habbema* has a high, domed braincase, depressed and concaved frontals, raised and fluted nasals and a squarish, 'dog-faced' rostrum. The left and right alisphenoid tympanic bullae are widely separated and very weakly enlarged. The foramina pseudovale are very large and are not bisected by a bridge of the alisphenoid. The eustachian canal opening is large and the entocarotid foramina are just anterior to the foramen pseudovale. The internal jugular canal foramina are small, the canals are low and obscure. The posterior lacerate foramina are large and exposed but the entocarotid foramina are small and hidden. The premaxillary vacuities extend from the level of the I^2 root back to the level of the posterior edge of the C^1 root. The large maxillary vacuities extend from the level of the metacone root of M^1 and back to the level of the protocone root of M^4 . Single large palatine vacuities (left and right) occur posterior to the maxillary vacuities.

SYNONYM

Antechinus hageni Laurie, 1952 (Figs 4, 5)

HOLOTYPE. BMNH 50.1829, adult ♂ puppet skin and skull (both in excellent condition).

TYPE LOCALITY. Mt Tomba, SW slopes of Hagen Range, Central Highlands, PNG, 05°50'S, 144°02'E, altitude 2,501m. Coll. F. Shaw Mayer, 30 June 1947.

The holotype differs from the holotype of *habbema* in the following respects.

Pelage (Fig. 4). It has a more luxurious fur covering than *A. habbema*. The fur of the mid-back is 12mm long with the basal 9.75mm Slate Color, median 1.25 Clay Color and the apical 1mm black. Medially-thickened Fuscous Black guard hairs are up to 15.5mm long on the rump and reduce to 5.7mm where they terminate at the crown of the head posterior to the rhinarium. The tail is bicoloured with mid-dorsal hairs averaging 2.8mm (Clove Brown) and mid-ventral hairs averaging 5.8mm (Olive Buff). At the tail tip, dorsal hairs are as long as 5.3mm (Clove Brown) while the ventral crest hairs are up to 13.5mm (Olive Buff).

Hindfoot. The left hind foot hallucal and post-hallucal pads are fused, while in the right foot they are separate. Auxillary apical granules occur outside first and third interdigital pads on left and right hind feet. A post, third-interdigital granule occurs on left and right hind feet.

Dentition (Fig. 5). Teeth are unworn and allow description of features lost in the *habbema* type.

Upper Incisors: I^1 is narrow, needle-like, slightly procumbent with an extremely high crown. Left and right I^1 are widely separate and the tops of the crowns are directed away from each other in the direction of the dentary line. It is difficult to detect a gradation of crown size in the upper incisors, but it appears as if I^4 crown is larger than I^3 which is larger than I^2 . All are weakly cingulated buccally. I^1 has no anterior or posterior cusp.

Upper Canines: C^1 is very long and slender with an extremely weak buccal cingulum indicating the very high crown, at least mid-way up the exposed tooth.

Upper Premolars: $P^3 > P^2 > P^1$. All carry strong buccal cingula but no lingual cingula. All are spaced, with contact occurring only between M^1 and P^3 . There is no posterior cusp on P^3 .

Upper Molars: The posterior tip of P^3 is in the parastylar corner of M^1 but lingual to, and just below stylar cusp A in the left dentary, and level with stylar cusp A in the right dentary. Stylar cusp A is prominent. The anterior cingulum of M^1 is very broad and complete, and stylar cusp B is much greater in mass than the paracone. There is a small protoconule present as well as a small bulge of enamel directly below it on the face of



FIG. 3. Holotype of *Antechinus habbema* Tate & Archbold, 1941 (now *Micromurexia habbema*). AMNH 109812, cranium and dentary. Sex = m; BL = 26.75; ZW = 16.51; IO = 7.73; OBW = 10.71; IBW = 4.46; R-LC¹ = 5.14; R-LM¹ = 9.30; R-LM² = 11.10; R-LM³ = 13.08; R-LM¹T = 7.35; M²W = 1.71; I¹-M⁴ = 14.70; P¹⁻³ = 3.35; M¹⁻⁴ = 6.24; Dent = 21.38; I₁-M₄ = 12.87; P₁₋₃ = 3.57; M₁₋₄ = 6.81; M₂W = 1.06.

the anterior protocrista. Styler cusps C and E are absent. There is no posterior cingulum.

In M² the anterior cingulum is very broad and complete as far as the small protoconule. Styler cusps A, C and E are absent. Styler cusp D is tall in M², and is considerably taller than in M¹. There is no posterior cingulum present.

In M³ the anterior cingulum is broad and complete but narrow at the base of the paracone. Styler cusps A, C and E are absent and D is reduced to a low cutting crest.

In M⁴ the protocone is reduced but still relatively broad. There is some metacone development although this is minimal and does not constitute a true metacone. It is such that in occlusal view the angle made between the post-protocrista and the premetacrasta is close to 80°.

Lower Incisors: In crown height I₁ is greater than I₂ which is greater than I₃. I₃ is premolariform in lateral view with a very low open notch formed by primary and secondary cusps.

Lower Canines: C_1 slender, tall, erect, with very slight curvature from root to crown, with very weak buccal and lingual cingulation. Diastema between C_1 and P_1 is equal to that between P_1 and P_2 which is greater than the diastema between P_2 and P_3 . P_3 touches M_1 . In overall size P_2 is larger than P_3 which is larger than P_1 .

Lower Molars: The anterior cingulum on M_1 is very poorly developed and the paracristid (in lateral view) is vertical from the paracristid fissure to the protoconid. The cristid obliqua is long and extends from the hypoconid to the posterior wall of the trigonid intersecting the trigonid at a point directly below the protoconid tip. Hypocristid is complete from hypoconulid to hypoconid. The entoconid is very large.

In M_2 the talonid is equal in width to the trigonid. There is a slight buccal cingulum. The very tall entoconid is of equal height to the paraconid. The cristid obliqua extends from the hypoconid to the posterior trigonid wall intersecting the trigonid at a point lingual to that point directly below the protoconid tip but buccal to that point directly below the metacristid fissure.

In M_3 the trigonid is wider than the talonid. The cristid obliqua intersects the trigonid at a point well lingual to that point directly below the tip of the protoconid but buccal to the point directly below the tip of the metacristid fissure.

In M_4 , although there is greater reduction in the 'buccal cingulum' than in the holotype of *habbema*, the 3 cusps of the talonid — the entoconid, hypoconulid and hypoconid are very well developed and prominent.

Skull (Fig. 5). As for the holotype of *habbema* but in *hageni* the premaxillary vacuities extend from the I^2 root back to the level of the middle of the C^1 root. The large maxillary vacuities extend from the level of the protocone root of M^1 and extend back to the level of the metacone root of M^3 . There are no palatine vacuities.

ADDITIONAL DIAGNOSTIC FEATURES

Micromurexia habbema differs from all other dasyurids in the combination of: 1, extremely thin, spur-like crown in I^1 which is needle-like and only slightly procumbent; 2, a slightly cingulated upper incisor row where $I^2 < I^3 < I^4$; 3, extremely long, thin, needle-like upper canines in which the root and crown are undifferentiated, and in which there is no posterior cusp; 4, an upper premolar row in which the cingulated teeth are uncrowded yet in which P^1 and P^2 are slightly rounded with accompanying postero-lingual

lobing; 5, M^1 very broad, with wide protocone and complete anterior cingulum, the anterior margin of this tooth is straight or anteriorly convex, but never indented or concave; 6, M^1 stylar cusp B large and only slightly smaller than stylar cusp D; 7, M^4 protocone broad and anterior cingulum complete; 8, M^1 and M^2 stylar cusp D a relatively low crest rather than a tall cone; 9, M^1 metacone relatively large; 10, a poorly cingulated lower premolar row in which the narrow teeth are widely spaced and where P_3 is slightly smaller than P_2 ; 11, uncingulated P_3 ; 12, well-developed paraconid on M_1 ; 13, 3 well-developed cusps on M_4 talonid; 14, tall entoconid on M_2 ; 15, metacristids and hypocristids not transverse to the long axis of the dentary; 16, fluted nasals; 17, poorly developed tympanic wing of the alisphoid which is contrasted by an expanded pars mastoidea and adjacent squamosal; 18, skull markedly domed posterior of the frontals; 19, tail with small ventral crest along entire length, the tail being longer than the head-body length; 20, polyoestrous, and only 4 nipples.

In addition to the diagnosis, *habbema* differs significantly ($P < 0.001$) from *P. naso* as follows (measurements are means, mm): shorter total length TL (246:275); shorter tail T (135:149); shorter ear length E (16.95:18.40); shorter basicranial BL (26.70:30.13); narrower zygomatic ZW (15.56:17.45); narrower outside bullae OBW (10.43: 11.57); narrower inside bullae IBW (4.72: 5.81); narrower rostral widths $L-RC^1$ (5.00:5.91), $L-RM^1$ (8.87:10.57), $L-RM^2$ (10.49:12.97), $L-RM^3$ (12.76:15.48); shorter upper tooth row I^1-M^4 (15.02:17.32); shorter upper premolar row P^{1-3} (3.85:4.63); narrower upper second molar M^2W (1.73:2.02); shorter dentary Dent (21.46: 24.23); shorter lower tooth row I_1-M_4 (13.12: 15.18); shorter lower premolar row P_{1-3} (4.08:4.73); narrower lower second molar M_2W (1.11:1.31); semi-straight, slender claws rather than strongly curved and thick; tail well-haired dorsally and ventral crest hairs long throughout rather than tail almost naked dorsally with weaker ventral crest developing at the tip. The likely presence of auxiliary apical granules outside the interdigital pads of the hind feet and non-fused hallucal/post-hallucal pads, rather than no auxiliary granules and always fusion between hallucal and post-hallucal pads; the tip of the tail skin never white, often white in *P. naso* (49%).

M. habbema differs significantly ($P < 0.001$) from *Mu. melamurus* by ear length E (16.95: 15.83); narrower zygomatic width ZW

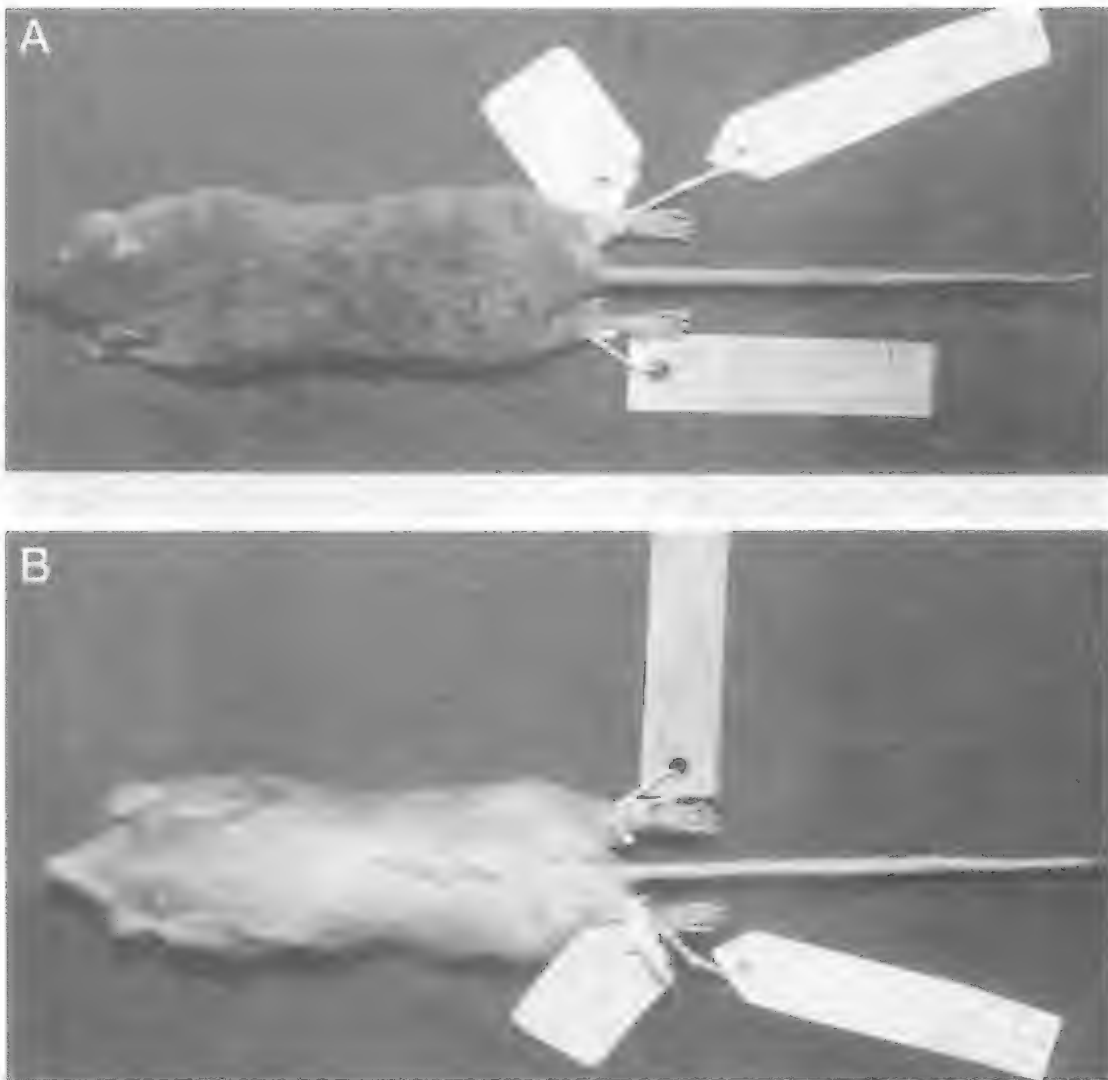


FIG. 4. Holotype of *Antechinus hageni* Laurie, 1952 (now *Micromurexia habbema*). BMNH 50.1829, study skin; A, dorsal view; B, ventral view. TL=234mm; HB=109mm; TV=125mm; HF=21mm; E=17.5mm.

(15.56:16.89); broader interorbital width IO (7.62:7.09); narrower postcranial width measured outside bullae OBW (4.72:5.12); narrower width inside bullae IBW (4.72:5.12); narrower rostral widths L-RC¹ (5.00:5.43), L-RM¹ (8.87:9.71), L-RM² (10.49:11.91), L-RM³ (12.76:14.12); longer upper premolar row P¹⁻³ (3.85:3.37); shorter upper molar row M¹⁻⁴ (6.38:6.78); narrower upper second molar M²W (1.73:1.89); longer lower premolar row P₁₋₃ (4.08:3.45); shorter lower molar row M₁₋₄ (6.86:7.37); narrower lower second molar M₂W (1.11:1.22); the likely presence on the hind foot

of auxiliary apical granules and unfused hallucal/post-hallucal pads rather than no auxiliary apical granules and always fused hallucal/post-hallucal pads.

M. habbema differs significantly ($P < 0.001$) from *Murexia longicaudata* by: shorter dentary DL (21.46:36.17); shorter tail T (135:197); shorter ear E (16.95: 20.50); semi-straight slender claws rather than strong, thick, curved claws; tail well-haired dorsally with long ventral crest throughout rather than semi-naked tail with very weak ventral crest; silky fur rather than short spinous fur; hindfoot without the post metatarsal

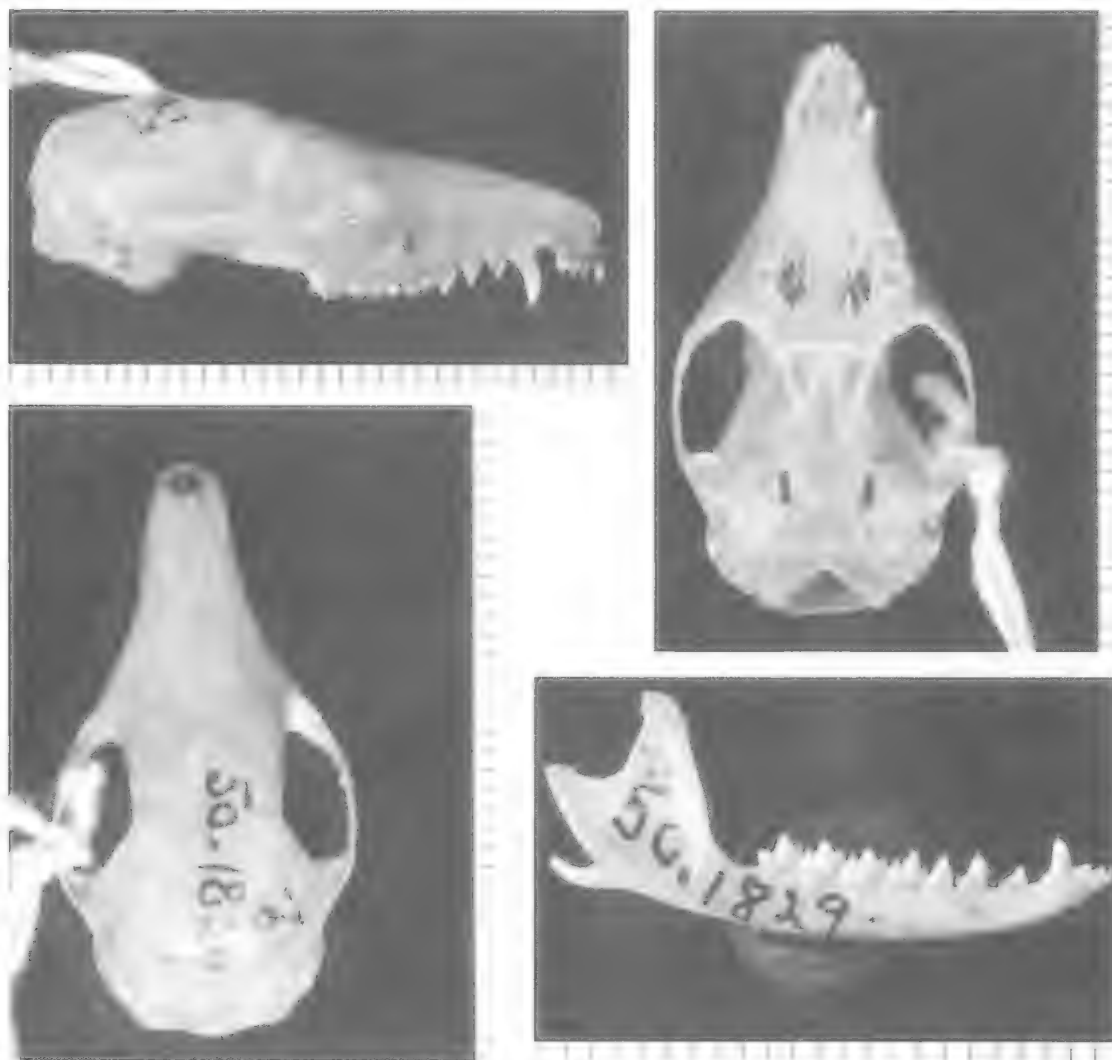


FIG. 5. Holotype of *Antechinus hageni* Laurie, 1952. BMNH 50.1829, cranium and dentary. Sex = m; BL = 27.71; ZW = 16.00; IO = 7.78; QBW = 10.86; IBW = 4.90; R-LC¹ = 5.24; R-LM¹ = 9.57; R-LM² = 11.18; R-LM³ = 13.27; R-LM¹T = 7.50; M²W = 1.69; I¹-M⁴ = 15.58; P¹⁻³ = 4.18; M¹⁻⁴ = 6.24; Dent = 22.26; I₁-M₄ = 13.58; P₁₋₃ = 4.43; M₁ = 6.75; M₂W = 1.11.

pads often present in *longicaudata*; the likely presence of auxiliary apical granules on the hind foot, rather than no auxiliary apical granules.

M. habbema differs significantly ($P < 0.001$) from *P. rothschildi* as follows: shorter upper premolar row P¹⁻³ (3.85: 4.77); shorter dentary Dent (21.46: 28.33); shorter tail T (135: 168); shorter hind foot HF (22: 27); shorter ear E (16.95: 19.92); semi-straight, slender claws rather than strongly curved claws; hindfeet lack post-metatarsal pads.

REMARKS. *Taxonomic History.* Six years after *Antechinus habbema* was described, Tate (1947) announced that he and Archbold had inadvertently described the species from a mismatched skin and skull. To remedy the situation Tate (1947) proposed to restrict use of *habbema* to the skin of the holotype which he, in turn, made a junior synonym of the species *mayeri* (originally described as *tafa centralis*, here regarded as *Phascomurexia naso*). The skull he assigned to a new species, *A. wilhelmina* (here regarded as

Murexechinus melanurus) which he described in the same paper.

The description of *hageni* Laurie, 1952, from Mt Tomba (Hagen Range), 550 km E of the type locality of Tate & Archbold's *habbema* (Lake Habbema, Irian Jaya), was quickly followed by Laurie & Hill's (1954) submersion of *hageni* into Tate's *wilhelmina*. Laurie's synonymy was followed thereafter, and subsequent references to the third New Guinea 'antechinus' species (the others being *naso* and *melanurus*) have been made under *wilhelmina* e.g., Honacki et al. (1982), Corbet & Hill (1980), Kirsch & Calaby (1977), Ziegler (1977), Baverstock et al. (1990). Other authors (Westerman & Woolley, 1993; Woolley, 1994; Krajewski et al., 1996; Armstrong et al., 1998) regard *wilhelmina* as a fourth New Guinea species of 'antechinus' (with *habbema*, *naso* and *melanurus*). I have examined the holotype of *habbema*, *hageni*, *tufa centralis* and *wilhelmina* and I have no doubts that, despite the similarities in skins of the 2 former and skulls in the 2 latter species, Tate was mistaken in his assumption that a mismatch had occurred. Justification for the retention of *habbema* as the senior synonym, and the rejection of Tate's assumption is as follows.

The skin. External body dimensions (e.g. HB, TV, E, HF) for the skin of the *habbema* holotype are at odds with those of the *tufa centralis* holotype and the series. The *habbema* holotype is an old adult ♂ in which the combined head, body and tail length is 252 mm. While this is average for the series of adult *habbema* males (N=26), only two adult males from the entire *naso* series (i.e., *naso*, *tufa*, *tufa centralis*, *mayeri misim*, *Murexia longicaudata parva* types and series, N=26) were recorded with such a low corresponding value. Even few adult females of *M. naso* (2 of 22) had corresponding values as low. The hind foot measurement of the *habbema* holotype is given as 21 mm. No male examined in the entire *naso* series (N=25) had a hind foot as small as the *habbema* holotype. Ear (crown) measurements for the *habbema* holotype is given as 13 mm. No specimen of *naso* for which crown-ear measurements were provided (N=12) had an ear as small as 13 mm.

The tail of the *habbema* holotype is well-haired with relatively long hairs dorsally (2 mm increasing to 4 mm near the tip) and a long ventral 'crest' (hairs 5 mm increasing to 7 mm near its tip [tip broken], 13 mm in the *hageni* holotype). This compares badly with the typically semi-naked tail of the *tufa centralis* holotype where dorsal

hairs are very short (uniformly 1 mm) as are hairs on the ventral crest (3 mm) but increasing to 14 mm at the ventral tip (see Figs 6, 7).

The hind feet of *habbema* are narrow in comparison to feet of *tufa centralis*. The original description of the *habbema* holotype emphasised this quality, 'Differing by the much smaller, more delicate feet and hands ... the width of foot across base of 5th metatarsal, 3.7, in *A. t. centralis*, 5.1, and in the type of *A. t. tufa* (f), 4.3.' (Tate & Archbold, 1941:9). Claws of the pes of *habbema* are semi-straight, thin and short in comparison to the stronger, thicker and more noticeably curved claws (which results in them looking shorter from above) of *tufa centralis* (see Fig. 7).

The skull. In the holotype of *wilhelmina* (and for *melanurus* as a whole) I¹ is broad, slightly procumbent, claw-like and curved posteriorly. In the holotype of *A. habbema* (and for the species) I¹ is narrow and needle-like with a minute crown (can be better seen in the *hageni* holotype which is relatively unworn). I²⁻⁴ in the *wilhelmina* holotype are blade-like and robust with buccal and lingual cingula. In the *habbema* holotype I²⁻⁴ are poorly cingulated, narrow and with minimal lingual curving of the crown.

C¹ in the *wilhelmina* holotype is heavy and short but caniniform. In the *habbema* holotype the canine is extremely long and slender with a very short crown.

The upper premolar row (in particular P¹⁻²) in the *wilhelmina* holotype is characterised by wide, robust premolars crowded into a relatively short row. In the *habbema* holotype the premolars are long, uncrowded and narrow, with P¹ separated from P² by a small diastema.

Lower molars (M₂, M₃, M₄) in the *wilhelmina* holotype lack entoconids. These however are well developed in the holotype of *habbema*. The *wilhelmina* holotype also lacks the complex M₄ talonid of the *habbema* holotype with its 3, well-developed cusps.

Flagging confidence in Tate's decision to synonymise the skull of *habbema* with *wilhelmina* is further aggravated by his comment (Tate, 1947:131) that 'Furthermore the skull which was associated with the type skin of *A. habbema* exactly matches the skulls of *A. wilhelmina*'. He also failed to rationalise the other 4 specimens which, with AMNH 109812, comprised the type series, and he made no comment regarding the corresponding mismatched *tufa centralis* skull and *wilhelmina* skin which must have generated from the initial 'mismatch'. Even

if Tate had actually mismatched the *habbema* skin and skull and there was still doubt about the distinction of the *habbema* skin, the skull alone exhibits all the features characteristic of a species which mark it as neither *naso* nor *melanurus* (including *wilhelmina*).

DISTRIBUTION. *M. habbema* is known from mid to upper-montane areas of the central cordillera (4°05'–8°03'S and 138°50'–146°53'E), central Irian Jaya to central Morobe Province, PNG (Fig. 8). It occurs at altitudes of 1600–3660m and has been collected in rain-forest, mid-mountain forest, beech forest, mossy forest and subalpine grassland. Full floristic details of collection localities appear in Archbold et al. (1942: 263–266) and Brass (1964: 189–216).

REPRODUCTION. All pouches examined contained 4 teats. Lactating ♀♀ had been collected in (date included in parenthesis) June (25), July (1, 3, 19, 24, 25, 27), August (no dates), October (31), November (7). No specimens (♂ or ♀) were examined which had been collected in December, January, February, March, April or May. Woolley (1994) recorded 2 lactating ♀♀ in December.

DESCRIPTION. *Mean Measurements* (mm). External: total length (head, body, tail) (♂) 251 (♀) 240; tail (to cloaca) (♂) 135 (♀) 133; hindfoot (su) (♂) 22.22 (♀) 22.15; ear (notch) (♂) 17.26 (♀) 16.54. Skull: basicranial length (♂) 27.31 (♀) 25.97; M^{1-4} length (♂) 6.43 (♀) 6.30; M^2 width (♂) 1.75 (♀) 1.70 (Table 1).

P4. In *habbema* P^4 is 3-rooted (AMNH 190885, 190887, 190894, 190904, 190908). In AMNH 190885 RP^4 shows a poorly developed protocone while the paracone and metacone merge, LP^4 shows a well-developed protocone and paracone and metacone. Styler cusps are poorly developed. A similar pattern of development is seen in AMNH 1090887 but here styler cusp B and the metastylid are developed. P_4 may be double or single-rooted. Of 4 specimens examined for P_4 , 2 had single-rooted R and LP_4 and 2 had double-rooted R and LP_4 . All lowers were premolari-



FIG. 6. Tail morphology of holotypes of: *Antechinus habbema*, AMNH 109812 (below) and *Antechinus tafa centralis*, AMNH 109823 (above).

form, however those of AMNH 190885 showed signs of 3 small and triangularly arranged cusps.

Pelage. There is considerable variation in the pelage colour of study skins, however some of this may be due to bleaching induced by a period of storage in ethanol prior to skinning. In such specimens from the eastern extremity of the range (Mt Tomba AM M9562, 9566) skins are very light and appear almost golden brown with the black patch absent from the anterior corner of each eye and the tail colour much diluted.

Tail. The tail is well-haired, but not densely so. A ventral crest is present, and the colour of the tail varies from light (in the east) to black (in the west). In three specimens from Mt Wilhelm, AMNH 109808, 109810, 109813 the tail is more lightly coloured dorsally and the caudal brush is a darker Sepia. These specimens are also characterised by a more crowded, shorter, upper premolar row (contact between P^1 – P^2 , P^2 – P^3 , P^3 – M^1 , in 109813; P^2 – P^3 , P^3 – M^1 contact in 109810, 109808) and palatine vacuities.

Hind Foot. Variable. hallual and post-hallual pads may be completely fused, or completely unfused, or any intermediate stage of fusion. Left and right hind feet may differ in the one individual. There may be a large auxiliary granule outside the first and/or third interdigital pads. An auxiliary hallual (or 'post-first-interdigital') pad is also variable (Fig. 9; Table 2).

SPECIMENS EXAMINED. Bulldog Road, 2400m, 07°31'S 146°40'E (BMNH 96748); Collins Sawmill, 2300m, 05°59'S 145°25'E (AMNH 190919); Giluwe Mt., 2684 m, 06°03'S 144°53'E (CM 29, CM 37); Giluwe Mt., 2700–2750m,

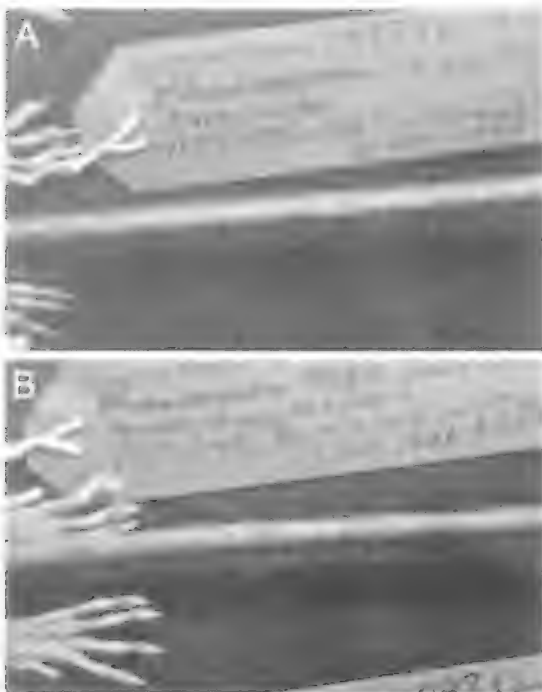


FIG. 7. Hind feet, tail and claws in the holotypes of: A, *Antechinus habbema*, AMNH 109812; and B, *Antechinus tafa centralis*, AMNH 109823.

06°03'S 144°53'E (BMNH53.204); Giluwe Mt., 2735m, 06°03'S 144°53'E (CM 12); Habbema Lake, 9km NE, 2706-2800m, 04°05'S 138°50'E (AMNH 152739); Habbema Lake, 9km NE, 2800m, 04°05'S 138°50'E (AMNH 109808, AMNH 109810, AMNH 109812, AMNH 109813); Hagen Mt., 2135-2400m, 05°54'S 144°09'E (AMNH 156370, AMNH 156372, AMNH 156373, AMNH 156389, AMNH 156391, AMNH 156393); Hagen Mt., 2592m, 05°54'S 144°09'E (AMNH 156367, AMNH 156376, AMNH 156395-156398); Hagen Mt., 3355-3660m, 05°54'S 144°09'E (AMNH 156378); Kaindi Mt., 2250-2350m, 07°21'S 146°43'E (BBM 29156, BBM 29183, BBM 29193, BBM 51049, BBM 51055, BBM 51073, BBM 51079, BBM 53411); Keglsugl, 2300m 05°50'S 145°06'E (AMNH 190880, BBM 100822); Marafunga, 2500-2350m, 05°58'S 145°08'E (BBM 55576); Marafunga, 2500m, 05°58'S 145°08'E (BBM 55562); Nondugl, 1600-1800m, 05°52'S 144°45'E (AMNH 183455, AMNH 222617); Nondugl, 1600-1800m, 05°52'S 144°45'E, (BMNH 56.7); Nondugl, 2135-2400m, 05°52'S 144°45'E, (AMNH 156364, AMNH 159392, AMNH 156394, AMNH 183594-183596); Nondugl, 2745-3660m, 05°52'S 144°45'E (AMNH 156361); Pengagl Creek, 2800m, 05°40'S 145°05'E (AMNH 190891, AMNH 190894, AMNH 190900, AMNH 190901, AMNH 190912); Smiths Gap, 2500m, 08°03'S 146°53'E (BBM 97023, BBM 97036); Tomba Mt., 2500m, 05°50'S 144°02'E (BMNH 50.1831, BMNH 50.1832, AM M9562, AM M9564, AM M9566); Tomba Mt., 2501m, 05°50'S 144°02'E (AMNH 50.1829); Wilhelm Mt., 2500-3570m, 05°46'S 144°59'E

(AMNH190881-190890, AMNH190892, AMNH 190896-190899, AMNH190902-190911, AMNH 190913-190918, AMNH100712); Wilhelm Mt., 2800m, 04°05'S 138°50'E (AMNH192270-76); Yanka, 1981m, 05°45'S 144°07'S (BMNH 50.1833).

Phascomurexia gen. nov.

Phascogale (in part) Temminck 1824.

Antechinus (in part) Macleay 1841.

Murexia (in part) Laurie 1952.

TYPE AND ONLY SPECIES. *Phascogale naso* Jentink, 1911: 236, based on RMNH 35134, adult ♂ puppet skin with skull, from Hellwig Mountains, Irian Jaya, 4°32'S 138°41'E at ~2,000m.

GENERIC DIAGNOSIS. M_1 very broad, with wide protocone and complete anterior cingulum, the anterior margin of this tooth is straight or anteriorly convex, but never indented or concave. Talonid on M_4 relatively unreduced. Tail longer than the head-body length.

It is distinguished from *Phascosorex* and *Myoictis* by its lack of dorsal body stripes, and from *Neophascogale* by its lack of reduced premolars and the lack of a thickly-haired tail.

Phascomurexia is separable from *Micromurexia* by the absolutely longer lengths of its upper and lower molar rows, $M1-4$.

Phascomurexia differs from *Murexechinus* by ears always lacking post-auricular patches rather than ears possessing rufous post-auricular patches; pelage uniform brown throughout rather than agouti with definite warming of tones toward rufous rump; tail semi-naked dorsally with weak ventral crest developing toward tip rather than tail well-haired dorsally with ventral crest hairs long throughout; I_1 narrow and needle-like rather than broad and claw-like; I_2-4 uncingulated rather than cingulated; I_1 long and slender rather than short and squat; premolar row long with un-crowded, narrow premolars rather than premolar row short with broad crowded premolars.

Phascomurexia is separable from *Murexia* by the shorter lower tooth row I_1-M_4 .

Phascomurexia naso is separable from *Paramurexia* by the narrower second upper and lower molars $M2$. *M. naso* also lacks a black dorsal body stripe.

Phascomurexia naso (Jentink, 1911) (Figs 10, 11)

Phascogale naso Jentink, 1911: 236.

Phascogale tafa Tate & Archbold, 1936: 3.

Antechinus tafa centralis Tate & Archbold, 1941: 8.

Antechinus mayeri misim Tate, 1947: 130.

Murexia longicaudata parva Laurie, 1952: 294.

Measurement		N	mean±r	OR	SD	V	CV
BL	Male	37	27.31±0.15	24.30-28.89	0.91	0.83	3.33
	Female	30	25.97±0.15	24.35-27.85	0.83	0.69	3.20
	Total	70	26.70±0.13	24.30-28.89	1.09	1.19	4.08
ZW	M	37	16.07±0.12	14.30-17.55	0.76	0.58	4.73
	F	27	14.92±0.10	13.77-15.92	0.53	0.28	3.55
	T	67	15.56±0.11	13.77-17.55	0.87	0.76	5.59
IOW	M	39	7.66±0.04	7.12-8.10	0.24	0.06	3.13
	F	30	7.55±0.04	6.99-7.90	0.20	0.04	2.65
	T	72	7.62±0.03	6.99-8.10	0.23	0.05	3.02
OBW	M	32	10.54±0.06	9.89-11.25	0.33	0.11	3.13
	F	27	10.28±0.07	9.59-10.88	0.38	0.15	3.70
	T	62	10.43±0.05	9.59-11.25	0.38	0.14	3.64
IBW	M	32	4.77±0.04	4.28-5.28	0.24	0.11	5.03
	F	27	4.67±0.05	4.32-5.30	0.24	0.06	5.14
	T	62	4.72±0.03	4.28-5.30	0.24	0.06	5.08
R-LC ¹	M	39	5.17±0.04	4.60-5.73	0.28	0.08	5.42
	F	30	4.81±0.03	4.53-5.33	0.17	0.03	3.53
	T	72	5.00±0.04	4.49-5.73	0.30	0.09	6.00
R-LM ¹	M	39	9.09±0.08	8.03-10.04	0.50	0.25	5.50
	F	30	8.58±0.06	8.20-9.57	0.31	0.09	3.61
	T	72	8.87±0.06	8.03-10.04	0.49	0.24	5.52
R-LM ²	M	28	10.68±0.10	9.79-11.92	0.54	0.29	5.06
	F	22	10.23±0.07	9.63-11.22	0.33	0.11	3.23
	T	53	10.49±0.07	9.63-11.92	0.51	0.26	4.86
R-LM ³	M	30	13.14±0.12	12.02-14.69	0.66	0.43	5.02
	F	23	12.24±0.08	11.66-13.09	0.38	0.15	3.10
	T	56	12.76±0.10	11.66-14.69	0.72	0.52	5.64
R-LM ¹ T	M	33	7.63±0.04	7.17-8.30	0.24	0.06	3.15
	F	26	7.37±0.04	7.04-7.89	0.18	0.03	2.44
	T	62	7.52±0.03	7.04-8.30	0.25	0.06	3.32
I ¹ -M ⁴	M	39	15.29±0.05	14.46-15.94	0.33	0.11	2.16
	F	30	14.66±0.07	13.70-15.85	0.41	0.17	2.80
	T	72	15.02±0.06	13.70-15.94	0.48	0.23	3.20
P ¹⁻³	M	40	3.94±0.05	3.35-4.72	0.30	0.09	7.61
	F	30	3.72±0.04	3.30-4.17	0.24	0.06	6.45
	T	73	3.85±0.03	3.30-4.72	0.29	0.09	7.53
M ¹⁻⁴	M	40	6.43±0.03	6.10-6.74	0.17	0.03	2.64
	F	30	6.30±0.03	6.00-6.63	0.16	0.03	2.54
	T	73	6.38±0.02	6.00-6.74	0.18	0.03	2.82
M ² W	M	40	1.75±0.01	1.45-1.89	0.08	0.01	4.57
	F	30	1.70±0.01	1.57-1.85	0.07	0.00	4.12
	T	73	1.73±0.01	1.45-1.89	0.08	0.01	4.62
Dent	M	39	22.08±0.19	19.20-27.71	1.20	1.45	5.43
	F	30	20.72±0.13	19.04-22.86	0.73	0.53	3.52
	T	72	21.46±0.14	19.04-27.71	1.22	1.48	5.68
I ₁ -M ₄	M	39	13.36±0.06	12.59-14.18	0.36	0.13	2.69
	F	30	12.83±0.09	12.20-14.68	0.47	0.22	3.66
	T	72	13.12±0.06	12.20-14.68	0.48	0.23	3.66
P ₁₋₃	M	40	4.23±0.05	3.57-4.94	0.29	0.09	6.86
	F	30	3.88±0.05	3.35-4.43	0.28	0.08	7.22
	T	73	4.08±0.04	3.35-4.94	0.33	0.11	8.09
M ₁₋₄	M	40	6.92±0.03	6.51-7.41	0.19	0.04	2.75
	F	30	6.78±0.03	6.57-7.11	0.15	0.02	2.21
	T	73	6.86±0.02	6.51-7.41	0.19	0.04	2.77
M ₂ W	M	40	1.12±0.01	1.05-1.25	0.04	0.00	3.57
	F	30	1.09±0.01	1.03-1.20	0.04	0.00	3.67
	T	73	1.11±0.00	1.03-1.25	0.04	0.00	3.60
TL	M	26	251±2.16	224-279	11.00	140.00	4.38
	F	19	240±1.38	229-260	6.00	43.00	2.50
	T	45	246±1.64	224-279	11.00	125.00	4.47
T	M	35	135±1.69	109-157	10.00	111.00	7.41
	F	22	133±1.28	119-143	6.00	47.00	4.51
	T	57	135±1.19	109-157	9.00	88.00	6.67
HF	M	34	22.22±0.28	19-25	1.61	2.58	7.25
	F	24	22.15±0.26	19.5-24	1.29	1.66	5.82
	T	58	22.19±0.19	19-25	1.48	2.20	6.67
E	M	31	17.26±0.17	15-19	0.97	0.93	5.62
	F	23	16.54±0.17	15-18	0.83	0.69	5.02
	T	54	16.95±0.13	15-19	0.98	0.96	5.78
W	M	15	34.59±1.07	28.35-45.36	4.14	17.10	11.97
	F	14	25.92±0.69	22.68-31.18	2.59	6.72	9.99
	T	29	30.40±1.03	22.68-45.36	5.55	30.85	18.26

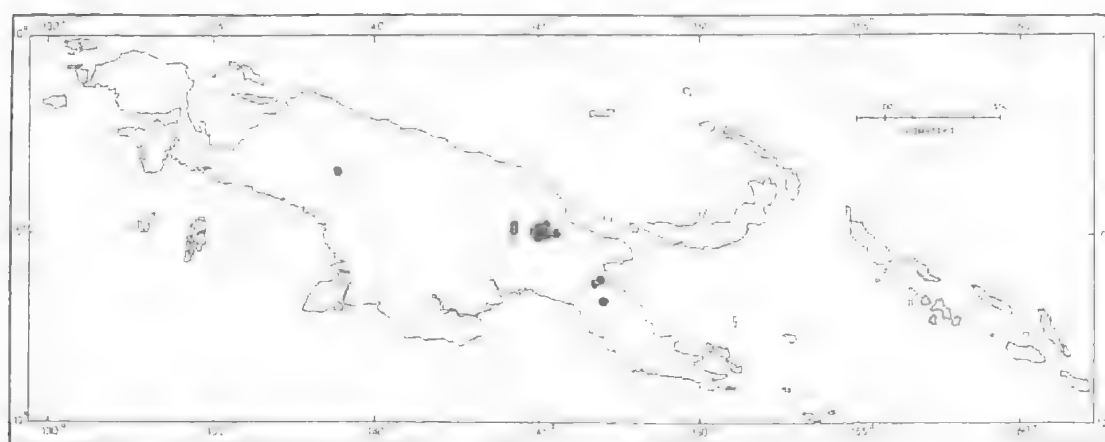


FIG. 8. Distribution of *Micromurexia habbema*.

HOLOTYPE. Rijksmuseum van Natuurlijke Historie, Leiden, RMNH 35134, Adult ♂ puppet skin and skull extracted (both in excellent condition).

TYPE LOCALITY. Hellwig Mountains, Irian Jaya, 4°32'S 138°41'E, ~2,000m. Coll. H.A. Lorentz, 16 October 1909.

DIAGNOSIS. As for genus.

DESCRIPTION. HOLOTYPE. *Pelage* (Fig. 10). Fur of the mid-back (8mm long) has basal 3mm Neutral Gray becoming Fuscous at 4.5mm, median 1mm Buffy Brown and apical 1.5mm Fuscous. The back appears to be a Greyish Sepia. Medially thickened guard hairs are interspersed through the fur and are 7mm long on the rump and reduce to 2.5mm at the crown of the head. Fur on and below the shoulders, thighs, flanks and chin lacks both black tips and the median Buffy Brown band and these areas appear Mouse Gray. The belly is Pale Olive-Buff and the fur is luxuriously soft, a pale grey becoming silvery-

white (not cream) along the belly mid-line. The fur is 7.5mm long on the belly and 6mm long on the interramal region with the basal 2/3 Light Neutral Gray and the apical 1/3 Pale Olive-Buff. It is interspersed with similarly coloured, medially thickened spines 7.5mm long. The forefeet are thinly covered with Hair Brown hair.

Hindfeet are more thickly covered with the same coloured hairs. The tail is weakly dorso-ventrally bicoloured with a very sparse covering of short hairs averaging 1.2mm (dorsally) along its length. These dorsal hairs are uniformly Sepia-coloured. Ventrally the hairs (3mm long near the base, increasing to form a ventral crest of hairs 6.5mm long) are coloured Ochraceous-Tawny.

Vibrissae. Approximately 20 mystaceal vibrissae occur on each side, up to 30mm long. The more dorsal mystaceal vibrissae are coloured Fuscous while those lower are colourless; supra-orbital vibrissae (Fuscous) number 0 left and 2 right;

TABLE 1. Absolute measurements for *Micromurexia habbema*. See 'Methods' for limits of measured dimensions. Abbreviations (as for Tables 3-6) are as follows: N = number of specimens in the sample; mean \pm 1 = sample mean \pm one standard error; OR = observed range; SD = standard deviation; V = variance; CV = coefficient of variation; M = male; F = female; BL = basicranial length; ZW = zygomatic width; IOW = interorbital width; OBW = basicranial width from outside right and left auditory bullae; IBW = distance between right and left auditory bullae; R-LC¹ = rostral width at the level of the upper canines; R-LM¹ = rostral width at the level of the first upper molars; R-LM² = rostral width at the level of the second upper molars; R-LM³ = rostral width at the level of the third upper molars; R-LM T = width between the ectolophi of right and left first upper molars; I-M¹ = length of upper tooth row (alveolar); P¹ = length of upper premolar row (alveolar); M¹ = length of upper molar row; M² = width of upper second molar; Dent = dentary length; I₁-M₁ = length of lower tooth row (alveolar); P₁ = length of lower premolar row (alveolar); M₁ = length of lower molar row (alveolar); M₂W = width of second lower molar; APV (not taken for all species) = anterior palatal vacuity length; PPV (not taken for all species) = posterior palatal vacuity length; IPV (not taken for all species) = inter-palatal vacuity length; NW (not taken for all species) = nasal width at the level of the premaxillary/nasal/maxillary junction; TL = total length, body and tail; T = tail length; HF = length of hind foot (su); E = length of ear (from notch); W = weight in grams.

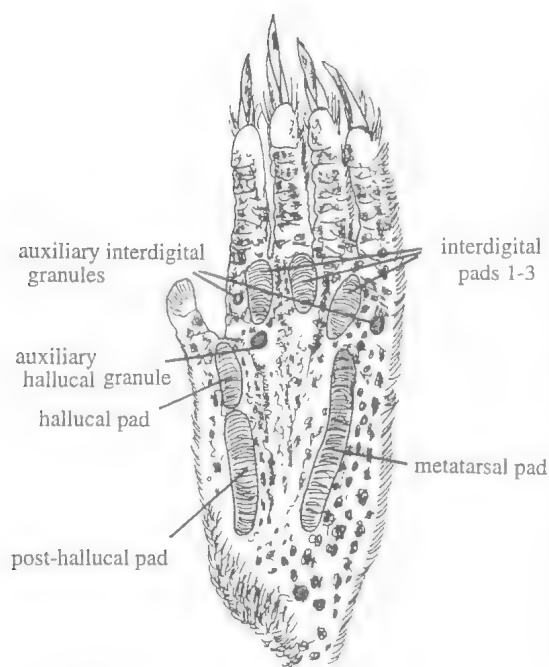


FIG. 9. Hindfoot padding in *Micromurexia habbema*.

genals (Fuscos and colourless) number 9 left and right; ulna-carpals number 5 left and right and submentals (colourless) number 4.

Tail. ~1.25 longer than the nose-vent length. It is thin and tapers toward the tip.

Hindfoot. The long hallucal and post-hallucal pads are narrow and fused. Interdigital pads are separate and the enlarged apical pad is elongate and striate. The metatarsal pad is very long and striate. The terminal pads of the digits are also striate.

Ears. The pinnae are large with a complex suprtragus which has a pronounced, thickened posterior margin and the distal end is reflected ventrally. The reflected tip is slightly concave.

Dentition (Fig. 11). Upper Incisors: I^1 is narrow, peg-like, slightly procumbent and relatively uncurved. R and LI^1 have crowns worn posteriorly so that the height of I^1 is equal to that of other upper incisors. I^1 is separated by a diastema from I^2 . R and LI^1 are obliquely inclined toward one another but contact does not occur. All upper incisors lack buccal and lingual cingula yet there is no lack of differentiation in root and crown. I^4 carries no anterior or posterior cusp. The roots of I^4 are narrow. In crown size I^4 is greater than I^3 which is greater than I^2 .

TABLE 2. Hindfoot morphology in *Micromurexia habbema*.

Hindfoot Condition		x/N	%
Right hallucal/post-hallucal pads	Unfused	69/89	77
	Fused	20/89	22
Left hallucal/post-hallucal pads	Unfused	71/90	79
	Fused	19/90	21
Right and left hallucal/post-hallucal pads	Unfused	66/90	73
	Fused	16/90	18
Right hallucal/post-hallucal fused, left Unfused		5/90	6
Left hallucal/post-hallucal fused, right Unfused		3/90	3
Auxiliary granules on both feet		51/69	74
No auxiliary granules on feet		9/69	13
Auxiliary granules on left foot only		6/69	8
Auxiliary granules on right foot only		3/69	4
Auxiliary granules on both feet		51/69	74
Right:			
# with granules at 1		5	10
# with granules at 3		9	18
# with granules at 1 and 3		37	72
Left:			
# with granules at 1		7	14
# with granules at 3		8	16
# with granules at 1 and 2		36	71
Aux. granules on left foot only		6/69	9
# with granules at 1		1	17
# with granules at 3		4	67
# with granules at 1 and 3		1	17
Aux. granules on right foot only		3/69	4
# with granules at 1		1	33
# with granules at 3		-	
# with granules at 1 and 3		2	67
Right feet, hallucal/post-hallucal pads:			
Fused, pads with aux. hallucal granule		1/7	14
Fused, pads without aux. granule		6/7	86
Unfused, pads with aux. granule		21/34	62
Unfused, pads without aux. granule		13/34	39
Left feet, hallucal/post-hallucal pads:			
Fused, pads with aux. granule		4/7	57
Fused, pads without aux. granule		3/7	43
Unfused, pads with aux. granule		25/33	76
Unfused, pads without aux. granule		8/33	24

Upper Canines: C^1 slender, erect, caniniform, with forward projection and an indistinct boundary between the root and crown. There is no buccal or lingual cingulum, and no anterior or posterior cusp. R and LC^1 have crowns broken off and abnormal thegotic wear is evident on the anterior surface of both canines.

Upper Premolars: The premolar row is long and diastemata separate all premolars. C^1 and P^1 are, however, very closely approximated. P^3 contacts M^1 and the diastema separating P^1 and P^2 is largest. All premolars carry strong buccal cingula. Weak lingual cingula are found on P^1 and P^2 , but P^3 lacks a lingual cingulum. P^1 crown is shorter than P^2 which is shorter than P^3 . Small anterior cusps occur on P^1 and P^2 with a less discernible anterior cusp on P^3 . There are very small posterior cingular cusps on P^2 and P^3 . No upper premolars possess postero-lingual lobes.

Upper Molars: The posterior tip of P^2 rests in the parastylar corner of M^1 but lingual to and just below a weak stylar cusp A. The anterior cingulum below stylar cusp B is short, broad and complete. Stylar cusp B and the paracone are relatively unworn and a large protoconule is present at the base of the paracone apex. The protoconule is accompanied by a large bulge of enamel directly below it on the face of the anterior protocrista. The paracone is well developed and approximately half the height of the metacone. Stylar cusps C and E are not visible on either R or LM^1 . M^1 has an indistinct posterior cingulum. Stylar cusp D is large but erect and narrow, not contributing greatly to the bulk of endoloph enamel.

In M^2 a narrow, almost incomplete anterior cingulum contacts the metastylar corner of M^1 and tapers quickly as it progresses down and along the base of the paracrista and finally degenerates labially to the base of the paracone apex. A protoconule is present with an associated anterior protocrista bulge as in M^1 . M^2 lacks stylar cusps A, C and E. There is a very indistinct posterior cingulum and stylar cusp D is reduced and erect.

In M^3 the anterior cingulum is incomplete and narrower than that in M^2 . It becomes indistinct after covering 1/2 the distance between stylar cusp B and the base of the paracone. There is a small protoconule but no associated enamel bulge. Stylar cusp D is greatly reduced to a minute conical peak. Stylar cusp E is weakly present but C is absent.

In M^4 the parastylar corner is grossly developed. The broad anterior cingulum is complete but a posterior cingulum is absent. The protocone is very broad. In occlusal view the angle made between the post-protocrista and post paracrista is close to 135° indicating little metacone development.

Lower Incisors: L and RI_1 both show abnormal thegotic wear caused from ill-occluding L and RI^2 . I_1 and I_2 are oval in anterolateral view and gouge-like in occlusal view. In crown size I_1 is greater than I_2 which is greater than I_3 . I_3 has a posterior cusp at the base of the crest which descends posteriorly from the apex of the primary cusp. The lower canine rests against this posterior cusp. In occlusal view, a small notch separates the posterior cusp from the prominent posterolingual lobe, and the crown enamel of the primary and posterior cusps folds noticeably so that the crest of the two cusps bisects the tooth longitudinally.

Lower Canines: C_1 is caniniform and characterised by slight curvature and erect projection. It has weak buccal, and slightly stronger lingual cingulation and no posterior cusp. The posterior surface of LC_1 shows abnormal thegotic wear caused by the broken LC^1 .

Lower Premolars: P_{1-3} are unevenly spaced, a slight diastema separates C_1 and P_1 , a wider diastema occurs between P_1 and P_2 , but P_2 and P_3 almost contact. All premolars are weakly cingulated buccally and lingually. In crown size P_2 is greater than P_3 which is greater than P_1 . All premolars are relatively broad and elongate. All possess posterior cusps, none possess anterior cusps. The bulk of each premolar mass is concentrated posteriorly to the line drawn transversely through the middle of the two premolar roots.

Lower Molars: All lower molars are relatively broad. The M_1 talonid is wider than the trigonid and the anterior cingulum is poorly developed. It continues around the posterior base of the protoconid into a weak buccal cingulum. The narrow paraconid appears in occlusal view as a small, steeply-sided spur, the lingual edge of which makes no appreciable swelling on the endoloph. The paracristid is almost 45° to the horizontal from the paraconid to the paracristid fissure and vertical from fissure to protoconid. The metacristid is roughly oblique to the long axis of the dentary while the hypocristid is perpendicular. The cristid obliqua is very short and extends from the hypoconid to the posterior wall of the trigonid, intersecting the trigonid at a point slightly lingual to that point directly below the tip of the protoconid. The entoconid is well developed as is a high entocristid slung between entoconid and metaconid. From the base of the metaconid posteriorly, the talonid endoloph shows an appreciable lingual incursion of enamel from the line of the endoloph. The weak buccal

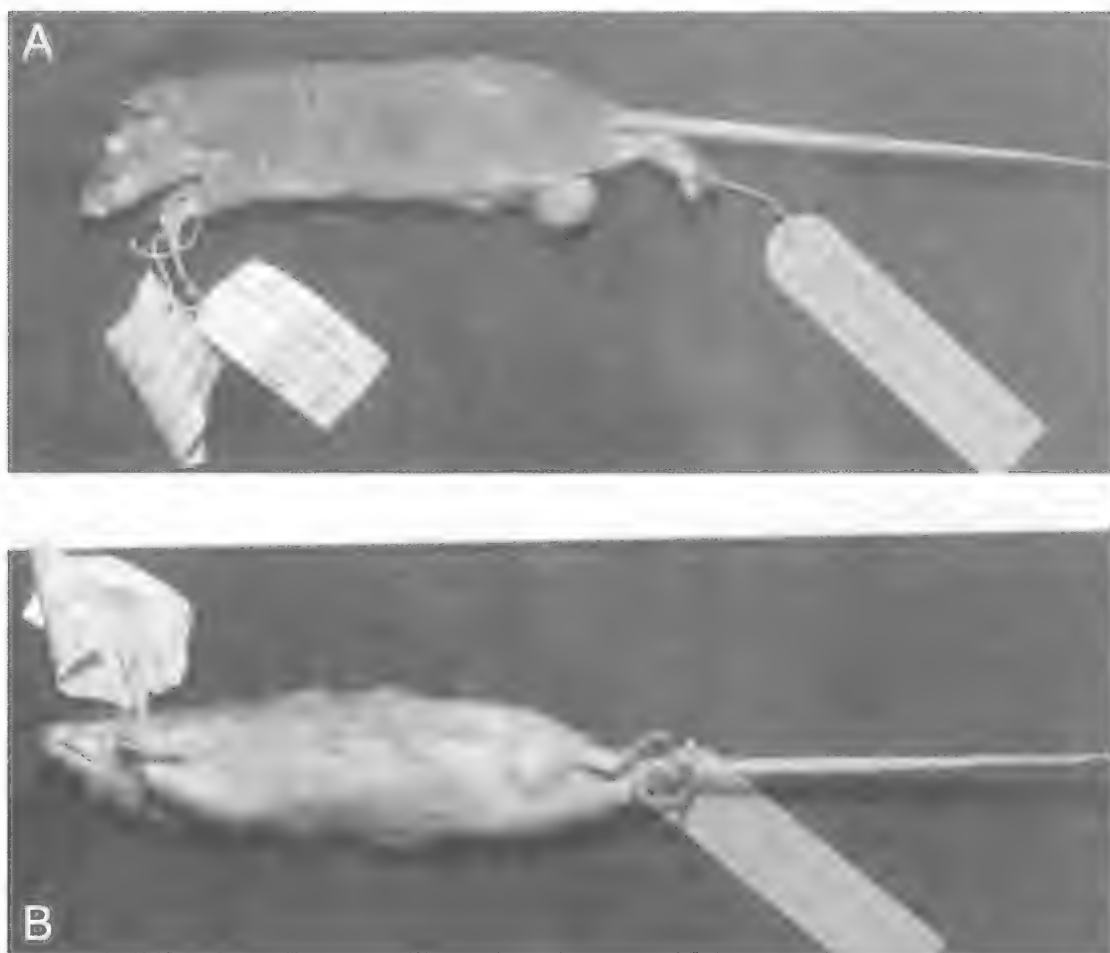


FIG. 10. Holotype of *Phascogale naso* Jentink, 1911 (now *Phascomurexia naso*). RMNH 35134, study skin; A, lateral view; B, ventral view. TL = 290mm; HB = 145mm; TV = 145mm; HF = 27mm; E = 16mm.

cingulum continues into a heavy posterior cingulum.

In M_2 the talonid is slightly narrower than the trigonid. The anterior cingulum is poorly developed but almost complete, breaking down just below the hypoconid. A narrow posterior cingulum extends from the hypoconulid to the posterior base of the hypoconid. The paraconid is well developed and is the smallest trigonid cusp. A large, broad entoconid is twice the height of the metastylid. The cristid obliqua extends from the hypoconulid to the posterior wall of the trigonid intersecting the trigonid at a point well lingual to that point directly below the protoconid tip but well buccal to the metacristid fissure. From the base of the metaconid posteriorly, the endoloph is characterised by a significant lingual swelling of the entoconid foundation.

In M_3 the trigonid is wider than the talonid. A prominent parastylid wraps around the hypoconulid of M_2 and there is a weak anterior cingulum on M_3 . Buccal and lingual cingula are continuous as in M_2 but weakly developed. The reduced cristid obliqua intersects the trigonid at a point well lingual to the longitudinal vertical midline drawn throughout the tip of the protoconid, but slightly buccal to the metacristid fissure. A large but worn entoconid is found on M_3 . The endoloph on the talonid of M_3 takes a more buccal orientation, under the reduced influence of a smaller entoconid, than that seen in M_2 . The rest of the morphology is as in M_2 .

In M_4 the trigonid is wider than the talonid. The anterior cingulum is as in M_2 . The posterior cingulum is absent. Of the three main trigonid



FIG. 11. Holotype of *Phascogale naso* Jentink, 1911 (now *Phascomurexia naso*). RMNH 35134, cranium and dentary. Sex m; BL 31.87; ZW 19.44; IO 8.22; OBW = 12.51; IBW = 6.60; R-LC¹ = 6.57; R-LM¹ = 11.29; R-LM² = 13.63; R-LM³ = 16.59; M³W = 2.00; I¹-M⁴ = 17.65; P¹⁻³ = 4.99; M¹⁻⁴ = 7.72; Dent = 26.16; I₁-M₄ = 15.72; P₁₋₃ = 4.66; M₁₋₄ = 8.28; M₂W = 1.36.

cusps, the metaconid is slightly taller than the paraconid but both are dwarfed by the protoconid. The hypoconid of M₄ is much more reduced than in M₃. Between the hypoconid and the base of the metacristid, the cristid obliqua forms a low, weak crest which contacts the trigonid wall directly below the metacristid fissure. A broad distinct M₄ buccal cingulum anchors the talonid to the trigonid. There is no entoconid, the hypoconulid is taller than the hypoconid and both are clearly distinct.

Skull (Fig. 11). The skull of the *naso* holotype has a high, domed brinca, depressed and concave frontals, greatly raised and fluted nasals and a squarish 'dog-faced' rostrum. The right and left alisphenoid tympanic bullae are widely separated and very weakly enlarged. The foramen pseudovale therefore appears very large and is not bisected by the inner wing of the entocarotid canal. The transverse canals are widely separated and just anterior to the foramen pseudovale. The eustachian canal foramina are large. The internal

jugular canal foramina are small, the canals low and obscure. The posterior lacerate foramina are large and exposed and the entocarotid foramina are large and exposed. The premaxillary vacuities extend from the level of the I^2 root back to $1/3$ the distance along the C^1 root. In the holotype, dry skin still covers the maxillary vacuities but they appear to be large, extending from the posterior root of P^3 to the protocone root of M^3 . It is impossible to detect palatine vacuities.

SYNONYMS

Phascogale tafa Tate & Archbold, 1936
(Figs 12, 13)

HOLOTYPE, AMNH 104050, adult ♀ (skin and skull in excellent condition).

TYPE LOCALITY. Eastern slopes of Mt Tafa, Central Division, PNG, $8^{\circ}22'S$ $147^{\circ}23'E$, at 2,130m. Coll. by R. Archbold & A.L. Rand, 25 May 1933.

The type of *tafa* differs from the *naso* holotype in the following respects.

Pelage (Fig. 12). The pouch area is stained rusty red and 4 elongated nipples are visible. The tail is more evenly haired than the *naso* type (which is sparsely haired almost to the point of patchy balding) and the last dozen hairs in *tafa* are white; there is, however, no white skin at the tip of the tail. Belly hair is slightly more silver and greater in extent than the more narrow band in the *naso* type.

Hindfoot. There are no significant differences in hindfoot morphology.

Dentition (Fig. 13). There are few significant differences in tooth morphology. R and L I^1 are unworn in *tafa* and in crown height I^1 is greater than all other incisors. I^1 is greater than I^3 which is greater than or equal to the height of I^2 . There is no abnormal wear on the upper canines, but their small size and straight carriage demonstrates the sexually dimorphic nature of canine size and shape in the species. The posterior cingula of M^{2-4} are more strongly developed, and styler cusps in M^3 are almost undetectable.

In the lower incisors RI^1 is missing, there is a slight, even gap between LP_1 , LP_2 and LP_3 , but RP_2 and RP_3 touch, thereby causing the diastema between P_1 and P_2 to be large. The rest of the molar morphology is as in the *naso* type.

Skull (Fig. 13). In AMNH 104050 the nasals are not raised as highly, or fluted to the same extent as in the *naso* holotype, the maxillary vacuities extend from the level of the posterior edge of the

M^1 protocone root back to the level of the M^3 protocone root. There are no palatine vacuities.

Antechinus tafa centralis Tate & Archbold, 1941
(Figs 14, 15)

HOLOTYPE, AMNH 109823, large adult ♂ (skin and skull in excellent condition).

TYPE LOCALITY. Bele River, 18km N of Lake Habbema, Irian Jaya, $4^{\circ}05'S$ $138^{\circ}42'E$. At 2,200m. Coll. W.B. Richardson, 17 November 1938.

The type of *tafa centralis* differs from *naso* in the following respects.

Pelage (Fig. 14). There are no significant pelage differences between the *tafa* and *tafa centralis* types. There are no white hairs in the tail crest.

Dentition (Fig. 15). There are few dental features in *tafa centralis* that differ significantly from *naso*. RI^1 is missing as is LP_1 . The only significant diastema in the upper premolar row occurs between P^1 and P^2 . In the lower right premolar row there is even spacing between all premolars and LP_3 is not in contact with LM_1 , however, in the lower left premolar row LP_3 contacts LM_1 .

Skull (Fig. 15). The nasals are lower and less fluted than in *naso*, and are more poorly developed than in *tafa*. Although the rostrum is typically high, the poor development of the nasals gives the top of the snout a flat appearance. Maxillary vacuities are large and wide, extending from the protocone root of M^1 back as far as the metacone root of M^3 .

Antechinus mayeri misim Tate, 1947
(Figs 16, 17)

HOLOTYPE, MCZ 29924, adult ♂ (skin and skull in excellent condition).

TYPE LOCALITY. Mount Misim, PNG, $7^{\circ}13'S$ $146^{\circ}50'E$. Altitude 1,784m. Coll. H. Stevens, 24 April 1933.

The type of *mayeri misim* differs from the type of *naso* in the following respects.

Pelage (Fig. 16). The fur is thin and silky, having the appearance of sparse pelage often seen in young dasyurids raised and weaned in captivity on an impoverished diet. The more typical luxurious fur in a female (MCZ 29923), collected in the same area two days after the *m. misim* type was collected, suggests that the sparse condition of the type may be abnormal. The tail is typically bare dorsally, but has been 'corkscrewed' around the wire used in the preparation of the study skin.

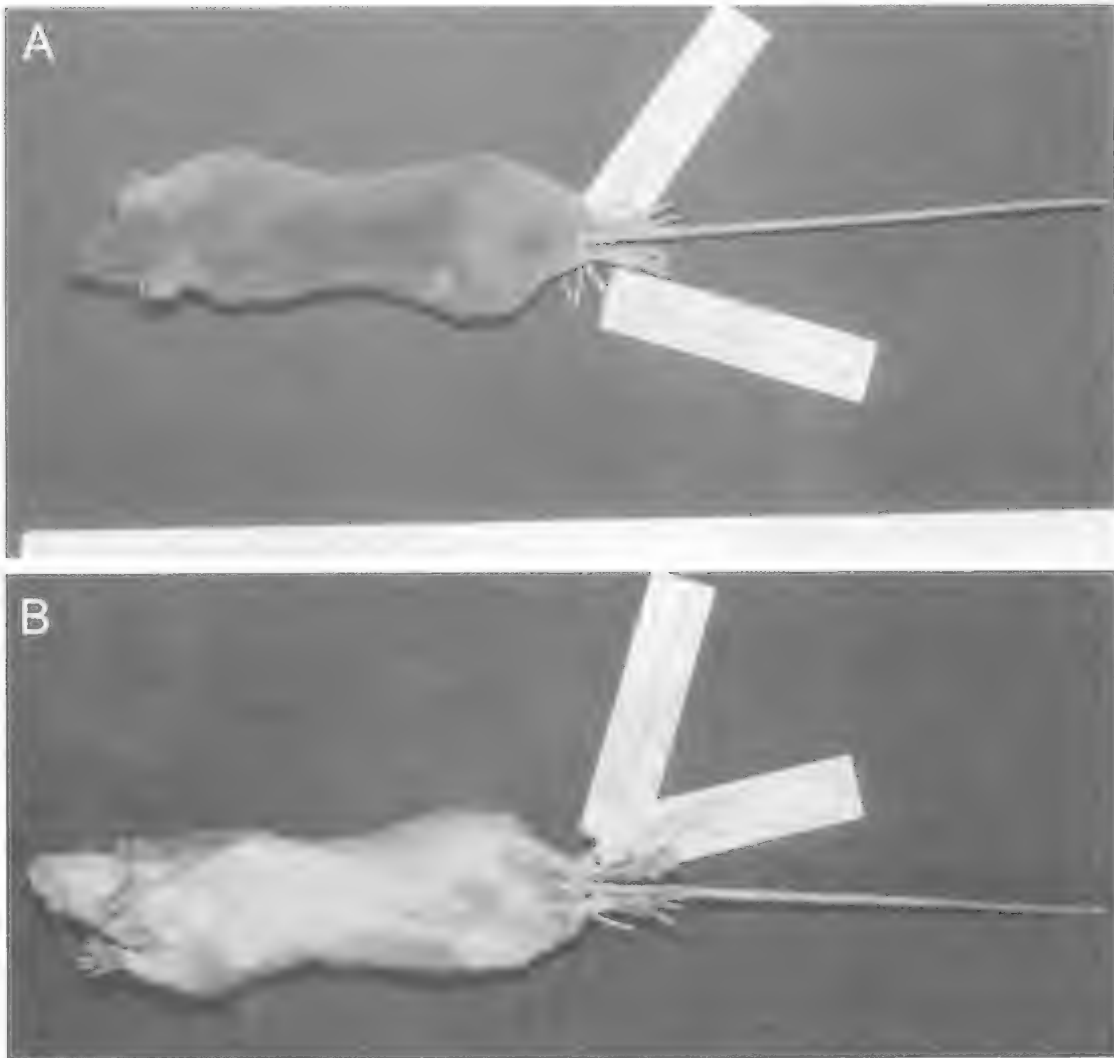


FIG. 12. Holotype of *Phascogale tafa* Tate & Archbold, 1936 (now *Phascomurexia naso*). AMNH104050, study skin; A, dorsal view; B, ventral view. TL = 279mm; HB = 134mm; TV = 145mm; HF = 25.

Dentition (Fig. 17). The *A. m. misim* type is a subadult male with emerging $P^3_{/3}$ and unworn dentition. L and RI^1 are widely separate and parallel. Unworn incisors show clearly I^2 crown lower than I^3 which is lower than I^4 , with no cusps. Paracone and styler cusp B appear closely approximated in M^{1-3} but this may be a function of youth and the lack of tooth wear. Upper and lower cingula are particularly weak throughout. There is no metacone development on M^4 . Entoconids are strongly developed on M_{2-4} and contribute greatly to the lingual bulging of the talonid endolophs. The subadult dentition suggests a very large animal when adult.

Skull (Fig. 17). Nasal fluting is minimal and both pre- and maxillary vacuities are long and broad. A small palatine vacuity occurs behind each maxillary vacuity.

Murexia longicaudata parva Laurie, 1952
(Figs 18, 19)

HOLOTYPE. BMNH 50.1114, adult ♂ (skin and skull in excellent condition).

TYPE LOCALITY. Baiyanka, Ramu River Divide, SE Bismarck Range, $5^{\circ}35'S$ $144^{\circ}51'E$. At 2,287m. Coll. F. Shaw Mayer, 6 June 1940.



FIG. 13. Holotype of *Phascogale tafa* Tate & Archbold, 1936. AMNH 104050, cranium and dentary. Sex = f; BL = 29.71; ZW = 17.06; IO = 7.67; OBW = 11.66; IBW = 5.64; R-LC¹ = 5.88; R-LM¹ = 10.35; R-LM² = 13.19; R-LM³ = 15.45; R-LM¹T = 8.27; M²W = 2.08; I¹-M⁴ = 17.20; P¹⁻³ = 4.46; M¹⁻⁴ = 7.51; Dent = 23.54; I₁-M₄ = 15.40; P₁₋₃ = 4.58; M₁₋₄ = 8.12; M₂W = 1.27.

The type of *longicaudata parva* differs from the holotype of *naso* in the following respects.

Pelage (Fig. 18). The fur is longer and more silky than the *P. naso* type. Guard hairs interspersed thinly through the fur are up to 10mm long on the rump and reduce to 5.6mm where they terminate at the crown of the head between the eyes. The

silver belly fur is much more extensive than that of the *P. naso* type. Hairs on the tail are long, averaging 1.2mm dorsally and 5mm long ventrally (mid-). At the ventral tip these hairs increase to 14mm long. The tail and hairs are white for the distal 23mm. Mystacial vibrissae number approximately 21 each side and are up to

33mm long. Supra-orbital vibrissae number 2 left and 2 right, genals number 8 left and 8 right; ulna-carpals number 3 right and 4 left and submetals number 6.

Dentition (Fig. 19). BMNH 50.1114 is a young specimen with only slightly worn dentition. R and LI¹ are slightly procumbent and while they are oriented toward one another they do not touch. I², I³ and I⁴ are subequal in crown height and length. C¹ is almost straight with no buccal or lingual cingulum. P³ is larger than P² which is larger than P¹. There is no anterior cusp on P³. M¹ has a strong posterior cingulum. In M² the anterior cingulum is narrow but complete. A protocone is present on the trigon basin and a small bulge of enamel on the face of the anterior protocrista accompanies it. Styler cusp D is just posterior to the metacone and a distinct posterior cingulum is present. In M³ the anterior cingulum is complete and broader than that of M². There is a prominent anterior cingulum at the base of the paracone and a small protoconule.

Styler cusp D is almost undetectable. Neither styler cusps C or E are present. In M⁴ the metastyler corner is well developed. The protocone is very broad and there is some prominent metacone development, making an angle of 90° between the posterior paracrista and the posterior protocrista. In the lower incisors, I₁ is much larger than I₃ which is equal to or slightly larger than I₂. There is an inconspicuous posterior cusp on I₃. The C₁ is only slightly curved and in the premolar row L and RP₂ are greater than P₃ which are greater in size than P₂. Small diastemata appear between LP₂ and LP₃, LP₃ and LM₁, LP₁ and LP₂, RP₂ and RP₃ and RP₁ and RP₂ (each side given in descending order of diastema magnitude).

In M₁ the cristid obliqua extends from the hypoconid to the posterior wall of the trigonid intersecting the trigonid at a point slightly buccal to that point directly below the tip of the protoconid. M₁ also shows a very well-developed entoconid. In M₃ the entoconid takes a great reduction in size and is absent in M₄.

Skull (Fig. 19). Nasal fluting and rostrum height are accentuated in the *M. l. parva* types. The large maxillary vacuities extend from the level of the protocone root of M¹ back to the metacone root of M³. A small palatine vacuity occurs posterior to each maxillary vacuity.

ADDITIONAL DIAGNOSTIC FEATURES

Phascomurexia naso differs from all other

dasyurids in the combination of the following features: 1, thin, spur-like crown in I¹ which is needle-like and almost procumbent; 2, uncingulated upper incisor row where I²<I³<I⁴; 3, long, thin (but bulkier and shorter than in *Micromurexia*) upper canines in which the root and crown are more differentiated than in *Micromurexia*, and in which there is no posterior cusp; 4, an upper premolar row in which the narrow, slightly cingulated teeth are uncrowded, and in which P¹ and P² are not rounded or postero-lingually lobed, nor does the P³ show a posterior cusp; 5, M¹ very broad, with wide protocone and complete anterior cingulum, the anterior margin of this tooth is straight or anteriorly convex, but never indented or concave; 6, M¹ styler cusp B very large and in M² only slightly smaller than styler cusp D, in some specimens styler cusp C is visible; 7, M⁴ protocone slightly more reduced than in *Micromurexia* and anterior cingulum complete; 8, M¹ and M² styler cusp D slightly heavier than in *Micromurexia*; 9, M¹ metacone relatively large; 10, heel of I₃ wider than that of I₁; 11, a lightly cingulated lower premolar row in which the narrow teeth are widely spaced and where P₃ is only slightly smaller than P₂; 12, cingulated P₃; 13, well-developed paraconid on M₁; 14, three poorly-developed cusps on the M₄ talonid; 15, tall entoconid on M₂ but very small or absent on M₄; 16, metacristids and hypocristids are not transverse to the long axis of the dentary; 17, very fluted nasals which, in lateral view, might be convex at the junction of the premaxillaries; 18, poorly developed tympanic wing of the alisphoid which is contrasted by a greatly expanded pars mastoidea and adjacent squamosal; 19, skull domed posterior of the frontals; 20, tail almost naked dorsally with weak ventral crest developing toward the tip (48% tails white-tipped); 21, polyoestrous and nipple number low (4).

In addition to those features noted in the diagnosis *naso* also differs significantly ($P<0.001$) from *M. habbema* as follows (measurements are means, mm); longer total length TL (275:246); longer tail T (149:135); longer ears E (18.40:16.95); longer basicranial length BL (30.13:26.70); greater zygomatic width ZW (17.45:15.56); wider outside bullae OBW (11.57:10.43); wider inside bullae IBW (5.81:4.72); wider rostral widths L-RC¹ (5.91:5.00), L-RM¹ (10.57:8.87), L-RM² (12.97:10.49), L-RM³ (15.48:12.76); longer upper tooth row I¹-M⁴ (17.32:15.02); longer upper premolar row P¹⁻³ (4.63:

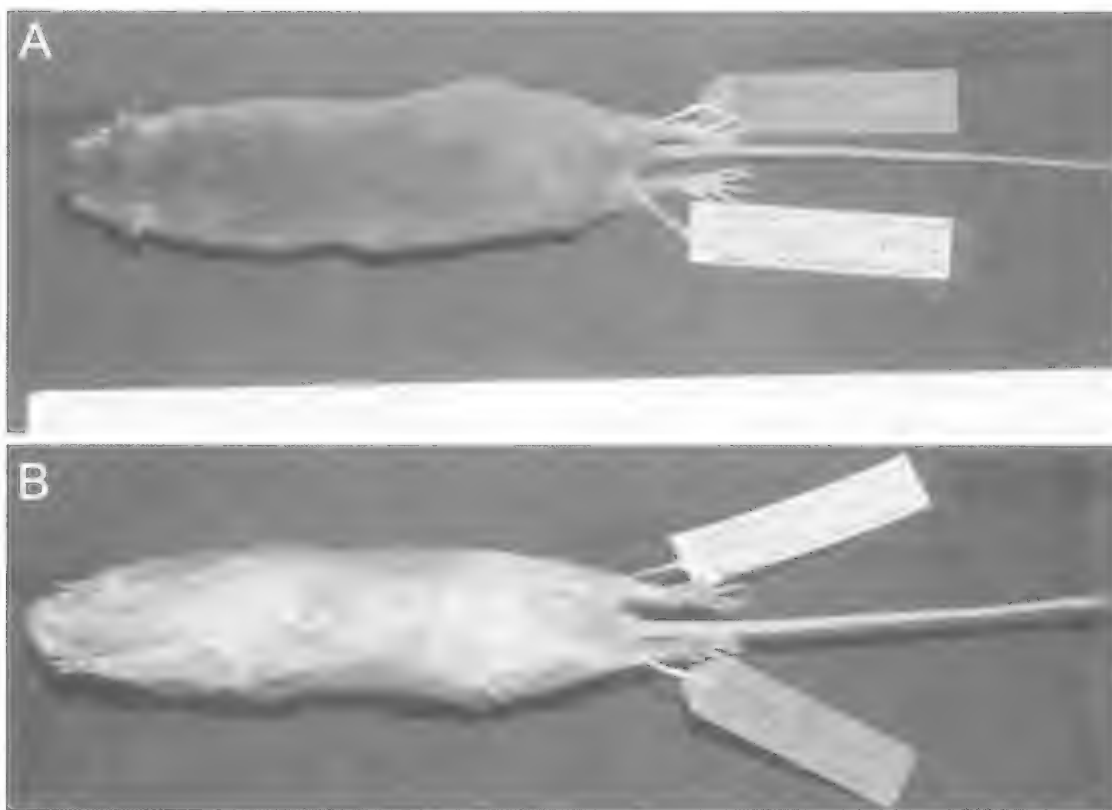


FIG. 14. Holotype of *Antechinus tafa centralis* Tate & Archbold, 1941 (now *Phascomurexia naso*). AMNH 109823, study skin; A, dorsal view; B, ventral view. TL=281mm; HB=135mm; TV=146mm; HF=26mm.

3.85); wider upper second molar M^2W (2.02:1.73); longer dentary Dent (24.23:21.46); longer lower tooth row I_1-M_4 (15.18:13.12); longer lower premolar row P_{1-3} (4.73:4.08); wider lower second molar M_2W (1.31:1.11); strongly curved, thick claws rather than claws semi-straight and slender; tail almost naked dorsally with weak ventral crest developing toward the tip rather than tail well-haired dorsally and ventral crest hairs long throughout; the absence of auxiliary apical granules on the interdigital pads of the hind feet and hallucal/post-hallucal pads always fused rather than the likely presence of auxiliary apical granules and non-fused hallucal/post-hallucal pads; the tip of the tail skin often white (48%) rather than never white (in *Micro. habbema*).

P. naso differs significantly ($P<0.001$) from *M. melanurus* as follows (measurements are means, mm): longer basicranial length BL (30.13: 26.83); wider interorbital width IOW (7.56: 7.09); wider inside bullae IBW (5.70: 5.12);

wider rostral widths R-LM¹ (10.57:9.71), R-LM² (12.97:1.91), R-LM³ (15.48:14.12); wider maxillary R-LM¹T (8.50:7.69); longer upper tooth row I^1-M^4 (17.32:14.88); longer upper premolar row P^{1-3} (4.63:3.37); longer upper molar row M^{1-4} (7.61: 6.78); wider second upper molar M^2W (2.02:1.89); longer dentary Dent (24.23:21.31); longer lower tooth row I_1-M_4 (15.18:12.96); longer lower premolar row P_{1-3} (4.73:3.45); longer lower molar row M_{1-4} (8.32:7.37); wider second lower molar M_2W (1.31:1.22); longer TL (275: 247); longer tail T (149: 133); longer hind foot HF (25.35:22.27); longer ear E (18.40: 15.83); the tip of the tail often white (48% of individuals examined) and usually lightly coloured throughout rather than tail always dark (dark brown to black) and never with white tip.

P. naso differs significantly ($P<0.001$) from *Murexia longicaudata* as follows: shorter basicranium BL (30.13: 43.64); narrower zygomatic width ZW (17.45: 25.33); narrower



FIG. 15. Holotype of *Antechinus tupa centralis* Tate & Archbold, 1941. AMNH 109823, cranium and dentary. Sex = m; BL = 31.92; ZW = 19.14; IO = 7.86; OBW = 12.12; IBW = 5.85; R-LC¹ = 6.75; R-LM¹ = 10.92; R-LM² = 13.49; R-LM³ = 16.63; R-LM¹T = 9.12; M²W = 2.03; I¹-M⁴ = 17.61; P¹⁻³ = 4.77; M¹⁻⁴ = 7.57; Dent = 26.16; I₁M₄ = 15.59; P₁₋₃ = 5.50 M₁₋₄ = 8.08; M₂W = 1.33.

outside bullae OBW (11.57: 14.59); narrower inside bullae IBW (5.81: 8.44); narrower rostrum R-LC¹ (5.91: 8.40), R-LM¹ (10.57: 14.71), R-LM² (12.97: 17.80), R-LM³ (15.48: 21.24); narrower maxillae R-LM¹T (8.50: 11.95); shorter upper tooth row I¹-M⁴ (17.32: 25.01); shorter upper premolar row P¹⁻³ (4.63: 7.49); shorter

upper molar row M¹⁻⁴ (7.61: 10.10); narrower second upper molar M² W (2.02: 2.75); shorter dentary Dent (24.23: 36.17); shorter lower premolar row P₁₋₃ (4.73: 7.92); shorter lower molar row M₁₋₄ (8.32: 10.90); narrower second lower molar M₂W (1.31: 1.71); shorter total length TL (275: 398); shorter tail T (149: 197);

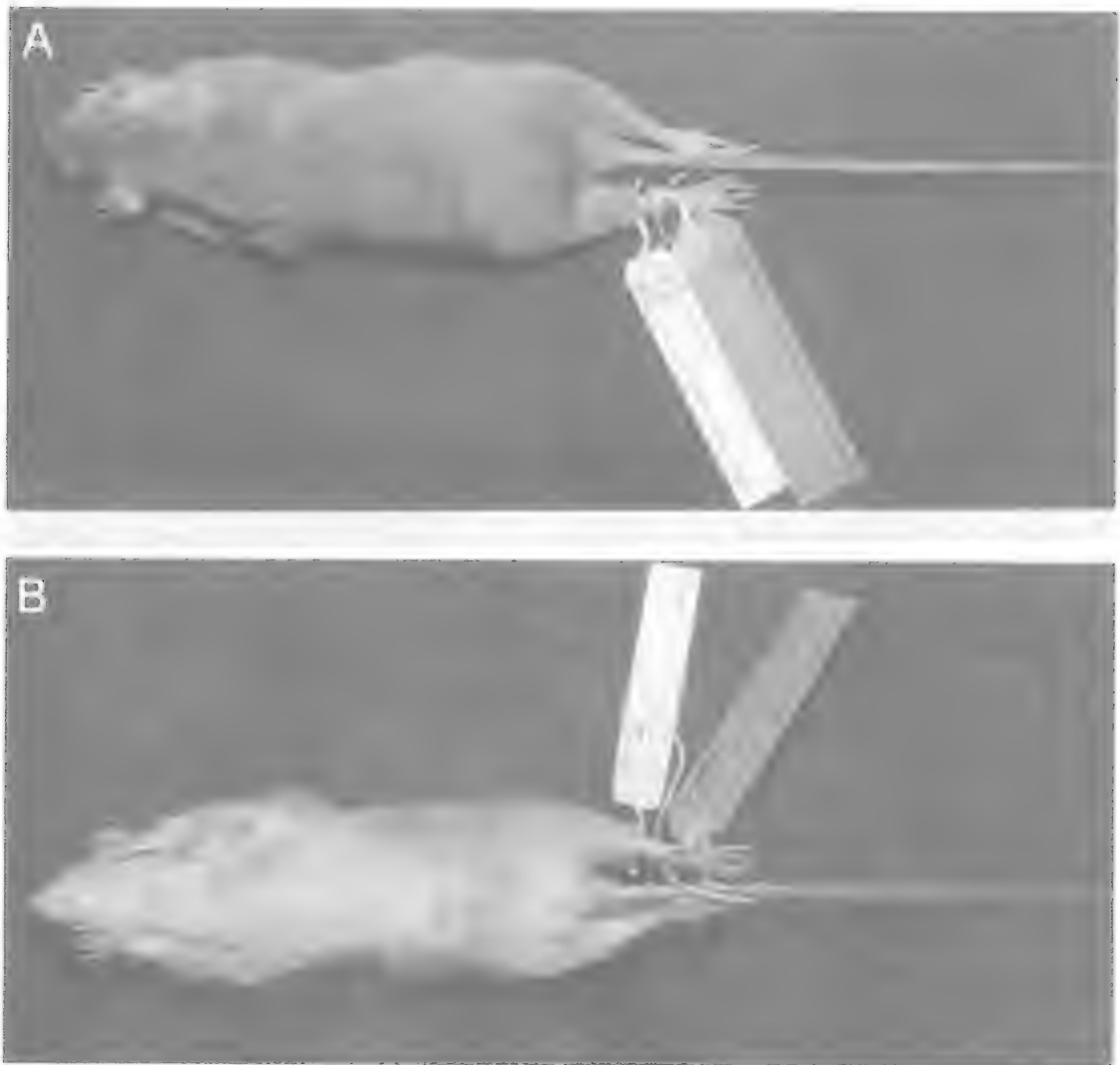


FIG. 16. Holotype of *Antechinus mayeri misim* Tate, 1947 (now *Phascomurexia naso*). MCZ 29924, study skin; A, dorsal view; B, ventral view. TL = 249mm; HB = 112mm; TV = 137mm; HF = 25mm.

shorter hind foot HF (25.35: 35.22); shorter ear E (18.40: 20.50); fur long and luxurious rather than short and harsh; ventral tail crest well developed rather than very poorly developed; no post-metatarsal granule on hind foot rather than well developed post-metatarsal granule often present.

Phascomurexia naso differs significantly ($P < 0.001$) from *Pa. rothschildi* as follows: shorter basicranial length BL (30.13: 35.41); narrower zygomatic width ZW (17.45: 21.29); narrower outside bullae OBW (11.57: 13.21); narrower inside bullae IBW (5.81: 7.27); narrower rostrum

R-LC¹ (5.91: 7.72), R-LM¹ (10.57: 12.20), R-LM² (12.97: 14.79), R-LM³ (15.48: 17.65); narrower maxillae R-LM¹T (8.50: 10.08); shorter upper tooth row I¹-M⁵ (17.32: 19.68); shorter upper molar row M¹⁻⁴ (7.61: 8.71); shorter dentary Dent (24.23: 28.33); shorter lower tooth row I₁-M₄ (15.18: 17.39); shorter lower molar row M₁₋₄ (8.32: 9.48); no post-metatarsal heel pads on hind foot rather than heel pads well developed.

REMARKS. *Taxonomic History*. It is strange that the disorder associated with the history of this species could have persisted as long as it did.

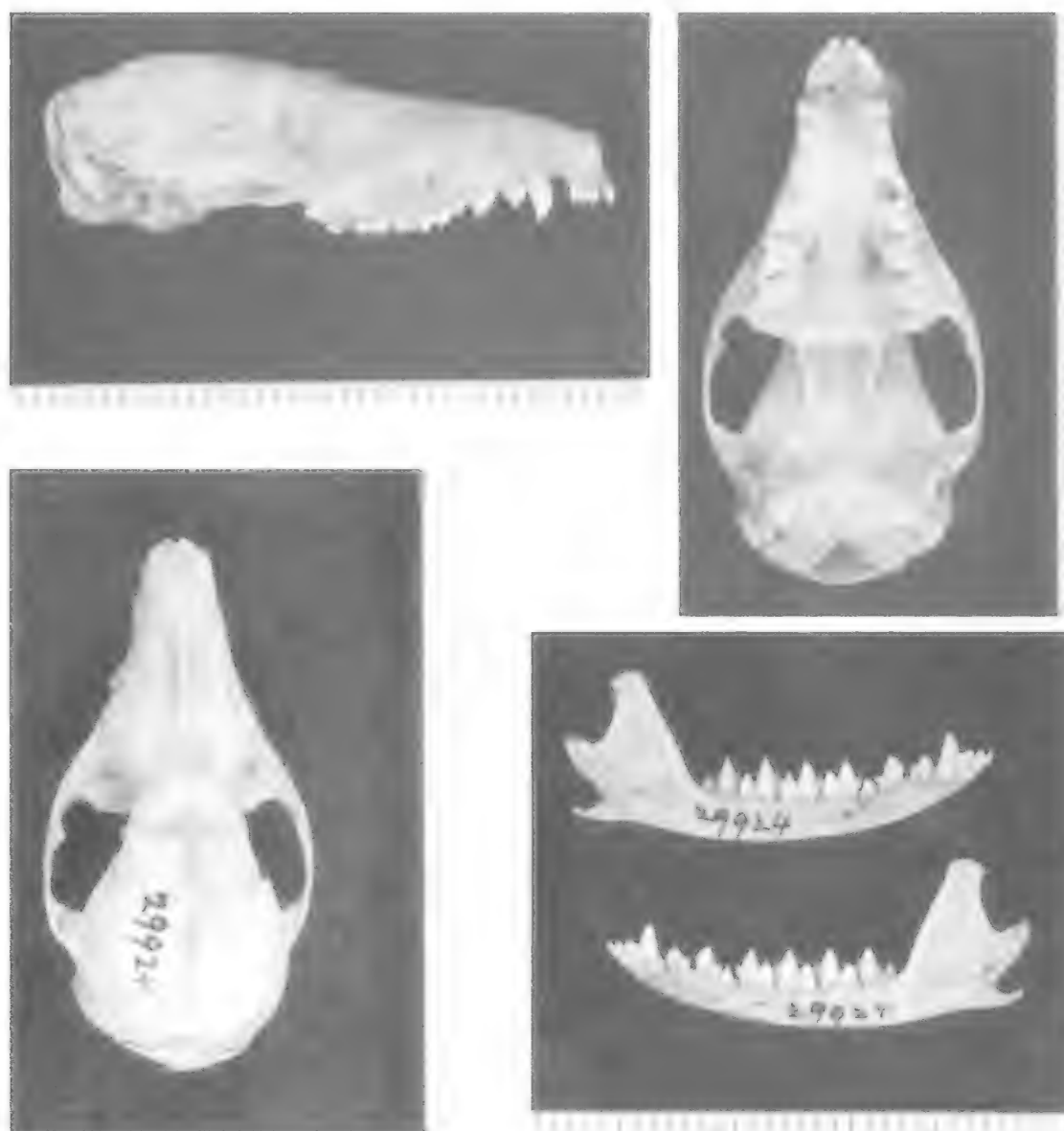


FIG. 17. Holotype of *Antechinus mayeri misim* Tate, 1947. MCZ 29924, cranium and dentary. Sex = m; BL = 30.81; ZW = 17.42; IO = 6.86; OBW = 11.94; IBW = 6.08; R-LC¹ = 5.93; R-LM¹ = 10.80; R-LM² = 13.33; R-LM³ = 15.48; R-LM¹T = 8.98; M²W = 2.29; I¹-M⁴ = 18.37; P¹⁻³ = 4.94; M¹⁻⁴ = 18.45; Dent = 24.99; I₁-M₄ = 17.10; P₁₋₃ = 4.76; M₁₋₄ = 9.74; M₂W = 1.43.

Jentink's original description of *naso* (1911) was more than adequate for its day considering the brevity of some type descriptions and obscurity of some journals (and newspapers) where many descriptions appeared. In addition, Jentink's specimen was (and still is) in extremely good condition. It is therefore remarkable that *naso* should have been virtually lost from the literature

for 43 years from the day of its description until its resurfacing in Laurie & Hill (1954).

Tate was aware of *P. naso* when he and Archbold described *P. tafa* (1936) — the two species were listed together by Tate as 'unplaced' forms ('... in the subgeneric sense ...' [Tate & Archbold, 1937: 339]). Tate's awareness of *naso* at this time was limited to Jentink's written

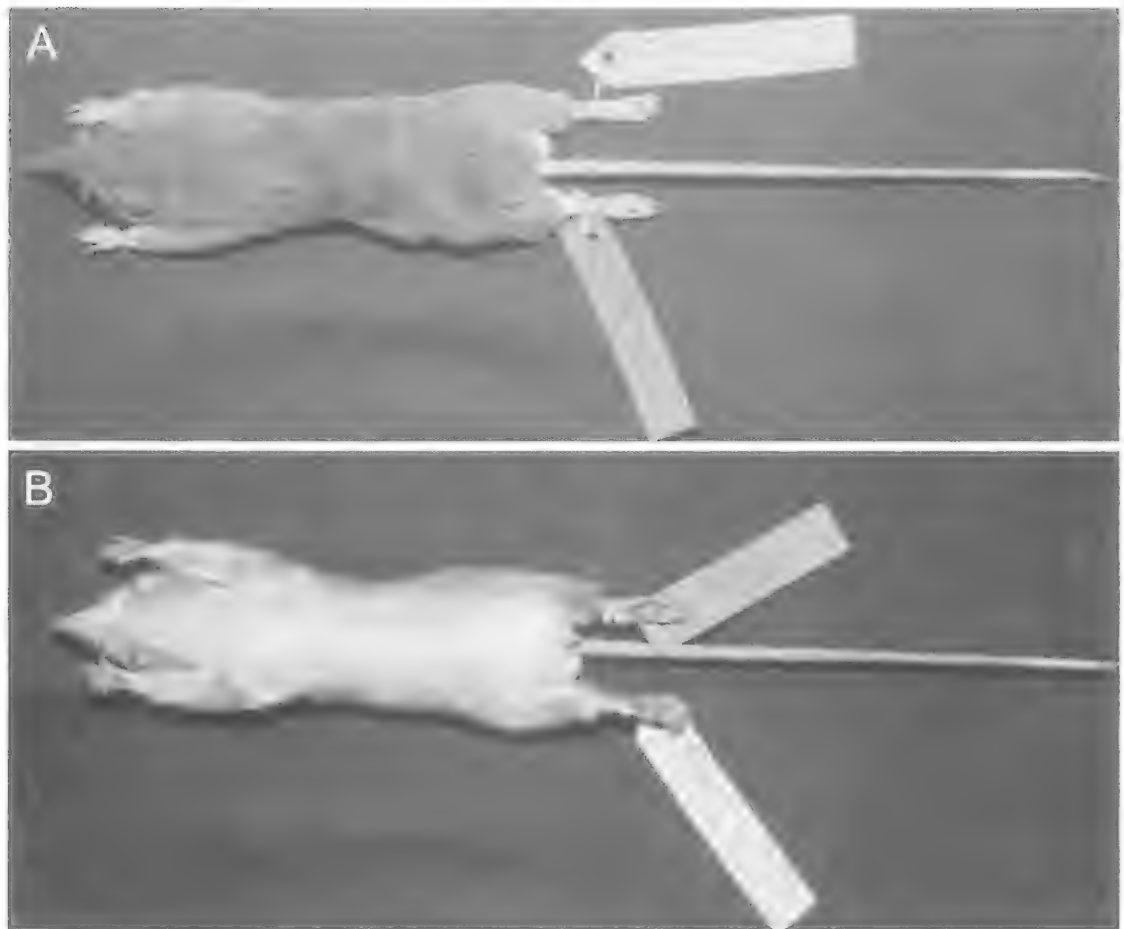


FIG. 18. Holotype of *Murexia longicaudata parva* Laurie, 1952 (now *Phascomurexia naso*). BMNH 50.1114, study skin; A, dorsal view; B, ventral view. TL = 307mm; HB = 132mm; TV = 175mm; HF = 26mm.

description as he had not, prior to 1937, examined type material in overseas institutions, and, as far as I am aware, the only other existing specimens (apart from the types of *tafa* and *naso*) were, presumably, 2 specimens collected by Stein in the Weyland Range, 1931 and held in East Berlin.

The specific title chosen by Jentink 1911, *naso*, drew attention to the fluted, raised condition of the nasals — ‘... so that a kind of small ram’s nose is imitated, giving the head of the animal a peculiar aspect, quite different from that of the other *Phascogale* - species’ (p. 236). Tate must have been strongly influenced by this part of the description and concluded that ‘The only species from New Guinea to which *rona* [*Sminthopsis virginiae*] might conceivably be allied is *naso* Jentink’ (Tate & Archbold, 1937:345; Tate & Archbold, 1936:2). Tate must have been unaware

of the variable nasal fluting in *naso* and, as AMNH 104050 exhibited reduced fluting, he evidently assumed it to be undescribed and published it as *tafa*. Hereafter (1937), *naso* was not referred to again by Tate.

It seems inconceivable that Tate could have missed the holotype of *naso* during his examination of types (*longicaudata*, *lorentzi*, *nouhuysii*, *melas*, *thorbeckiana*) in the Rijksmuseum van Natuurlijke Historie, Leiden (‘... I give some detailed measurements of the specimen [*Phascogale longicaudata*], made by me in Leiden ...’ Tate 1947: 117).

It is possible that Tate accidentally overlooked Jentink’s *naso* in the Leiden Museum, but it would be unkind to suggest a vague possibility that the potentially humiliating experience of discovering the real identity of *P. naso* in Leiden

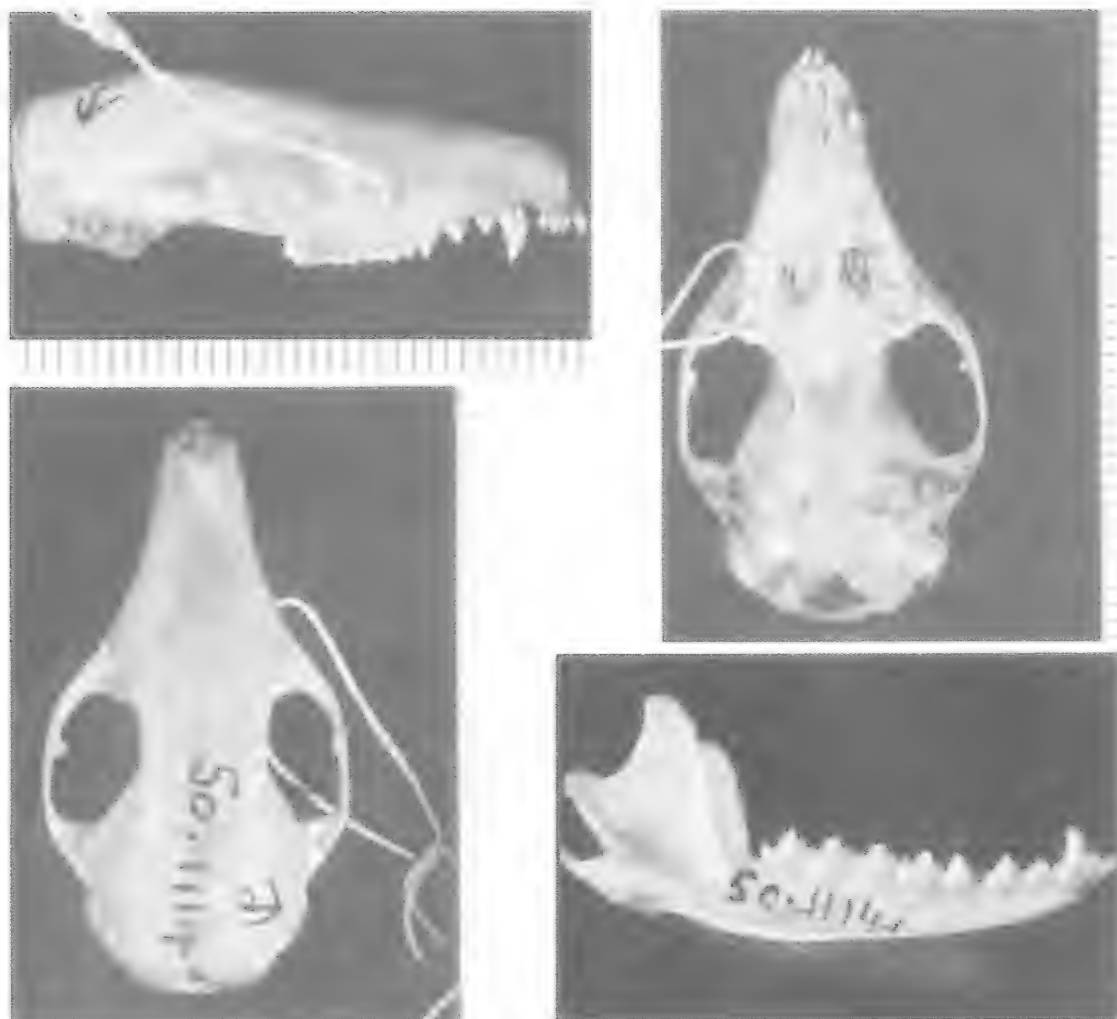


FIG. 19. Holotype of *Murexia longicaudata parva* Laurie, 1952. BMNH 50.1114, cranium and dentary. Sex = m; BL = 31.95; ZW = 19.06; IO = 7.63; OBW = 11.67; IBW = 6.25; R-LC¹ = 5.35; R-LM¹ = 11.16; R-LM² = 13.71; R-LM³ = 16.80; R-LM¹T = 8.97; M²W = 2.03; I¹-M⁴ = 18.27; P¹⁻³ = 5.20; M¹⁻⁴ = 7.89; Dent = 26.17; I₁-M₄ = 15.92; P₁₋₃ = 5.65; M₁₋₄ = 8.49; M₂W = 1.29.

just one year after describing *P. tafa* (Tate & Archbold, 1936) was too much for Tate's pride, and the specimen was academically overlooked from then on. Whatever the reason, it is most unlikely that Tate, after having examined the specimen, chose to ignore it because he could not come to grips with its identity and affinities.

In 1941, satisfied that *P. tafa* was eligible for subgeneric status of *Antechinus*, Tate & Archbold described *centralis*, a new subspecies of *tafa*. The specimen was a large ♂, considerably bigger than the ♀ *tafa* holotype. The subspecies was erected solely for 2 cranial

features: increased size of the maxillary vacuities and an increase in the internal width of the mesopterygoid fossa behind the palate (2 demonstrably variable characters in similarly sized animals). They admitted that the other size differences were due to sexual dimorphism within the species and that the new subspecies was '... separable from true *tafa* only by cranial characters ...' (Tate & Archbold, 1941: 8). The degree of nasal inflation and fluting in *centralis* was even more reduced than that of the *tafa* type, so it is not surprising that the name of *naso* again did not appear in association with this new form.

Six years later (in 1947) Tate submerged his and Archbold's species *tafa* (and *tafa centralis*) into Dollman's (1930) *mayeri*. This was done in spite of the following background to the decision:

1) that Dollman had indicated in his original description that *mayeri* was most closely allied to *melanurus*.

2) that Tate's examination of AMNH 101978 (typical *melanurus* features and which had been identified personally by Dollman as *mayeri*) convinced him and Archbold to (justifiably) relegate *mayeri* to subspecific status as *Phascogale (Antechinus) melanura mayeri* (Tate & Archbold, 1937).

3) that Tate had examined the holotype of *mayeri* — a specimen exhibiting all the dental and cranial features nominated by Tate (1947) to characterise specimens of *A. melanurus*. (The skin of *A. mayeri*, while lighter than typical *melanurus* displays rufous post-auricular patches and a long-haired, black tail, features which never appeared in any of Tate & Archbold's *tafa* types or in any of the AMNH series associated with them (see descriptions of *A. mayeri* (= *Murexechinus melanurus*) and *A. melanurus* (= *Murexechinus melanurus*) later for detailed cranial, dental and pelage data).

4) that Tate himself noted (1947: 128) the unusually low altitude from which the type of *mayeri* had come '... *mayeri* from only 3500 feet' (which is outside the range of *M. naso* but well within those limits ascribed by Tate to *M. melanurus*).

Then in the face of the very dubious separate identities of *A. mayeri centralis* and *A. mayeri tafa*, Tate added another subspecies, *misim* to the *mayeri* list. Once again here, another form was described which was externally '... indistinguishable from the races *centralis* and *tafa*' (Tate 1947: 130). The grounds for its subspecific status lay in its large teeth, and there can be no denying that up until the time of its description no other larger specimen appeared to exist. Tate made no mention, however, that this specimen was a subadult male with only newly emerging $P^{3/3}$, and although it was physically smaller than many other specimens which Tate had access to in his own collection, the large value of the dental measurements in the type description make it appear as if the specimen was of a unique form rather than of a young specimen whose large dental proportions would eventually match correspondingly large physical measurements at adulthood.

Tate's dilemma with his *mayeri* group of New Guinea dasyurids is best expressed in his own words, 'All four of these races stand so close to one another that later reviewers may decide that they should be merged together' (Tate, 1947: 129).

The encompassing confusion associated with Tate's dasyurid taxonomy is no more apparent than in his introduction to 'The Members of the *Antechinus flavipes* Group in New Guinea' (Tate 1947: 128). Here he summarised the characteristics of his three proposed groups of *Antechinus* in New Guinea: 1) *melanurus*; 2) *modestus*, *tafa*, *centralis*, *mayeri*; 3) *wilhelmina* (allusion to the name supplied later).

For inexplicable reasons, on the following page, Tate synonymised *modestus* (Thomas) with *melanurus* (Thomas) thereby lifting *modestus* from group 2 and adding it to group 1, and then introduced a further unmentioned '*misim*' to group 2 on page 130. A typographical error could explain the swapping of the names *modestus* for *misim* in the list of p. 128 but can not explain why *modestus* was omitted from group 1 with *melanurus*. If a typographical error had occurred it could be expected that the altitude data provided for *modestus* on p. 128 would simply correlate with that of the *misim* description on p. 130. These values are, however, different (5,000 and 5,850 feet respectively).

In 1952 Laurie described *Murexia longicaudata parva*, a large male of almost identical size to the type of *A. naso* (Jentink, 1911). It can only be assumed that Laurie's comparative assessment of the species was an 'in-house' process as no specimens other than her type and 5 paratypes existed in British Museum collections at the time of the description (or since). Unfortunately, at that time, many similar and some almost identical specimens were to be found in the collections of such natural history museums as the Rijksmuseum in Leiden, the Humboldt-Universitat in East Berlin and the American Museum (Natural History) in New York. Tate had never mentioned in his description of *A. tafa* that the last dozen hairs that comprised the tip of the long ventral crest were coloured white. Perhaps Laurie's attention would have been steered toward *P. naso* if this were the case. But despite this, in 1954 when Laurie and Hill's research revealed the valid identity of *A. naso* for *tafa*, *tafa centralis* and *mayeri misim* they not only failed to associate Laurie's *Murexia longicaudata parva* with Jentink's *naso* but they

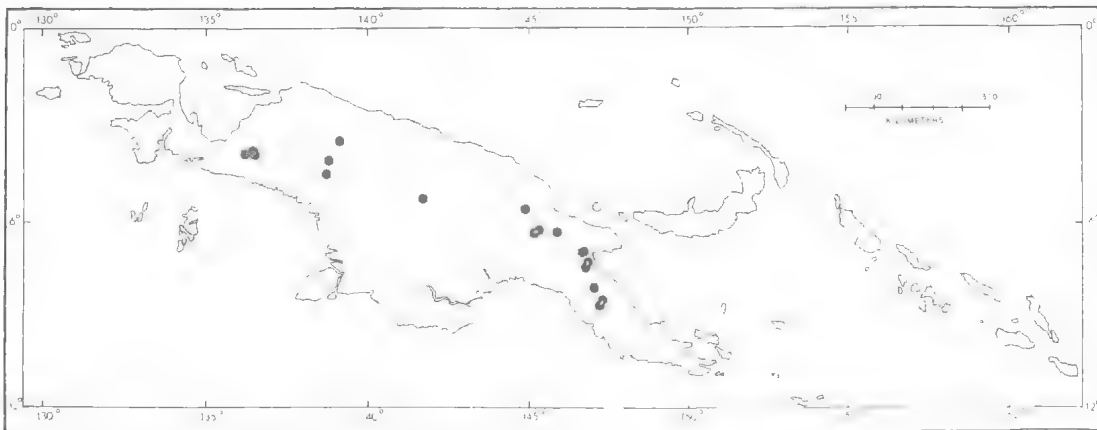


FIG. 20. Distribution of *Phascomurexia naso*.

also failed to recognise that the *A. mayeri* type (held in their own collection) was synonymous with *P. melanurus* and not with *naso*. Ziegler (1977) also referred to *naso* as including *mayeri*, but made a confusing reference (p. 125) to *mayeri* appearing in the '... list of Kirsch and Calaby' (1977) which actually contained the three New Guinea species *naso*, *wilhelmina* and *melanurus* without making a reference to *mayeri*. Honacki et al. (1982) note, however, that Ziegler recognised that *naso* '... probably includes *Murexia longicaudata parva*' (p. 28). And Archer (1982a), erecting the subfamily Murexinae, aired reservations about *M. l. parva* thus, '*Murexia longicaudata parva* is so similar in dental and cranial morphology to plesiomorphic species of *Antechinus* [New Guinea species] that the generic boundary can only be maintained by resorting to external morphology' (p. 428). Archer, in fact, was comparing not an example of *Murexia* with N.G. antechinuses, but another 'antechinus' — *A. naso*. Jenkins & Knutson (1983) assigned the holotype of *M. l. parva* in their care to *Murexia longicaudata*. Van Dyck (1982a) discussed the status and affinities of *A. godmani* and suggested a close phenetic relationship between *A. godmani* and *A. mayeri*. The use of the name *mayeri* by Van Dyck was ill-advised, coming from label names accompanying the specimens used in the comparison. The name *naso* should be substituted in all cases for *mayeri* in this work.

DISTRIBUTION. *Phascomurexia naso* is known from mid to lower montane areas of the central cordillera between 3°32'S 139°10'E Irian Jaya, and 8°35'S 147°09'E Central Morobe

Province, Papua New Guinea (Fig. 20). It occurs in a narrow altitudinal range from 1400–2800m and has been collected in rainforest, mid-montane forest, beech forest, pandanus forest and mossy forest. Full floristic details of collection localities appear in Archbold et al., (1942:246) and Brass (1964: 182).

REPRODUCTION. All pouches examined contained 4 teats. Lactating females had been collected in (dates including in parentheses), January (19), February (9), April (16, 29), May (19, 20), August (26), September (27). Dwyer (1977) noted the capture of lactating females in June (20) and December (13). Among other months mentioned already, Woolley (1994) noted lactating females from November.

DESCRIPTION. *Mean Measurements* (mm). External: total length (head, body, tail) (♂) 281, (♀) 268; tail (to cloaca) (♂) 152, (♀) 146; hind foot (su) (♂) 25.87, (♀) 24.83; ear (notch) (♂) 19.21, (♀) 17.65. Skull: basicranial length (♂) 30.79, (♀) 29.22; M^{1-4} length (♂) 7.64, (♀) 7.57; M^2 width (♂) 2.04, (♀) 2.01. (Table 3).

P₄ Morphology. 3 juveniles, AMNH 190872, 190873 and 152028. In two specimens P₄ was single-rooted and premolariform with a single cusp. In AMNH 152028 P₄ was double-rooted but again premolariform. P₄ was a single-rooted, formless spur.

Pelage and Tail. There is no reasonable justification for retaining subspecific groups within *P. naso*. There are however some variable features which deserve recognition. Tail colour varies not only with longitude but also greatly within specimens from eastern localities. Of 52

TABLE 3. Absolute measurements for *Phascomurexia naso*. See 'Methods' for limits of measured dimensions and Table 1 (caption) for abbreviations.

Measurement		N	mean \pm r	OR	SD	V	CV
BL	Male	22	30.79 \pm 0.43	27.17 - 33.74	2.02	4.08	6.56
	Female	16	29.22 \pm 0.16	28.07 - 30.42	0.63	0.39	2.16
	Total	38	30.13 \pm 0.29	27.17 - 33.74	1.77	3.13	5.87
ZW	M	21	17.99 \pm 0.29	15.51 - 20.28	1.35	1.83	7.50
	F	16	16.75 \pm 0.11	15.94 - 17.67	0.42	0.18	2.51
	T	37	17.45 \pm 0.20	15.51 - 20.28	1.22	1.50	6.99
IOW	M	22	7.75 \pm 0.07	6.92 - 8.26	0.31	0.10	4.00
	F	19	7.56 \pm 0.05	7.17 - 7.95	0.23	0.05	2.97
	T	41	7.66 \pm 0.05	6.92 - 8.26	0.29	0.09	3.79
OBW	M	22	11.76 \pm 0.11	11.05 - 12.74	0.50	0.25	4.25
	F	16	11.30 \pm 0.08	10.72 - 11.69	0.30	0.09	2.65
	T	38	11.57 \pm 0.08	10.72 - 12.74	0.48	0.23	4.15
IBW	M	22	5.89 \pm 0.09	4.98 - 6.60	0.41	0.17	6.96
	F	16	5.70 \pm 0.08	4.96 - 6.35	0.32	0.11	5.61
	T	38	5.81 \pm 0.13	4.96 - 6.60	0.39	0.15	6.71
R-LC ¹	M	22	6.10 \pm 0.10	5.26 - 7.01	0.48	0.23	7.87
	F	19	5.69 \pm 0.06	5.16 - 6.24	0.27	0.07	4.75
	T	41	5.91 \pm 0.07	5.16 - 7.01	0.45	0.20	7.61
R-LM ²	M	22	10.73 \pm 0.13	9.81 - 12.11	0.60	0.36	5.59
	F	19	10.39 \pm 0.14	9.60 - 12.24	0.62	0.39	5.97
	T	41	10.57 \pm 0.10	9.60 - 12.24	0.64	0.40	6.05
R-LM ³	M	19	13.17 \pm 0.19	11.76 - 14.62	0.82	0.68	6.25
	F	16	12.73 \pm 0.16	11.64 - 14.52	0.63	0.40	4.95
	T	35	12.97 \pm 0.13	11.64 - 14.62	0.77	0.60	5.94
R-LM ⁴	M	20	15.84 \pm 0.20	14.01 - 17.21	0.90	0.82	5.68
	F	16	15.03 \pm 0.16	13.92 - 16.85	0.63	0.40	4.19
	T	36	15.48 \pm 0.15	13.92 - 17.21	0.89	0.79	5.75
R-LM ² T	M	21	8.64 \pm 0.10	7.81 - 9.56	0.44	0.19	5.09
	F	19	8.34 \pm 0.08	7.87 - 9.11	0.36	0.13	4.32
	T	40	8.50 \pm 0.07	7.81 - 9.56	0.43	0.19	5.06
I ¹ -M ⁴	M	22	17.70 \pm 0.17	15.92 - 19.23	0.82	0.68	4.63
	F	19	16.89 \pm 0.14	15.85 - 18.85	0.59	0.35	3.49
	T	41	17.32 \pm 0.13	15.85 - 19.23	0.83	0.69	4.79
P ¹⁻³	M	22	4.83 \pm 0.11	3.80 - 5.90	0.50	0.25	10.35
	F	19	4.40 \pm 0.06	4.02 - 4.89	0.24	0.06	5.45
	T	41	4.63 \pm 0.07	3.80 - 5.90	0.45	0.20	9.72
M ¹⁻⁴	M	23	7.64 \pm 0.06	7.09 - 8.21	0.27	0.07	3.53
	F	19	7.57 \pm 0.08	7.15 - 8.69	0.34	0.11	4.49
	T	42	7.61 \pm 0.05	7.09 - 8.69	0.31	0.09	4.07
M ² W	M	23	2.04 \pm 0.01	1.90 - 2.22	0.07	0.01	3.43
	F	19	2.01 \pm 0.02	1.89 - 2.16	0.08	0.01	3.98
	T	42	2.02 \pm 0.01	1.89 - 2.22	0.08	0.01	3.96
Dent	M	22	25.03 \pm 0.29	21.73 - 26.93	1.36	1.85	5.43
	F	19	23.31 \pm 0.22	21.49 - 25.87	0.98	0.96	4.20
	T	41	24.23 \pm 0.23	21.49 - 26.93	1.47	2.17	6.07
I ₁ -M ₄	M	23	15.55 \pm 0.13	14.21 - 16.60	0.60	0.37	3.86
	F	18	14.70 \pm 0.08	14.01 - 15.40	0.32	0.10	2.18
	T	41	15.18 \pm 0.10	14.01 - 16.60	0.65	0.43	4.28
P ₁₋₃	M	22	4.96 \pm 0.10	3.91 - 5.72	0.48	0.23	9.68
	F	19	4.47 \pm 0.04	4.28 - 4.90	0.17	0.03	3.80
	T	41	4.73 \pm 0.07	3.91 - 5.72	0.44	0.20	9.30
M ₁₋₄	M	23	8.40 \pm 0.10	7.42 - 10.01	0.46	0.21	5.48
	F	19	8.22 \pm 0.08	7.60 - 9.24	0.34	0.12	4.14
	T	42	8.32 \pm 0.06	7.42 - 10.01	0.42	0.18	5.05
M ₂ W	M	23	1.32 \pm 0.01	1.24 - 1.43	0.04	0.00	3.03
	F	19	1.31 \pm 0.01	1.23 - 1.38	0.04	0.00	3.03
	T	42	1.31 \pm 0.01	1.23 - 1.43	0.04	0.00	3.05
TL	M	20	281 \pm 4.47	231 - 307	20	432	7.12
	F	18	268 \pm 2.36	247 - 285	10	101	3.73
	T	38	275 \pm 2.76	231 - 307	17	14	6.18
T	M	20	152 \pm 3.13	109 - 175	14	219	9.21
	F	19	146 \pm 2.29	126 - 164	10	111	6.85
	T	39	149 \pm 2.08	109 - 175	13	173	8.72
HF	M	19	25.87 \pm 0.33	23 - 29	1.45	2.10	5.60
	F	19	24.83 \pm 0.45	20 - 28	1.96	3.83	7.89
	T	38	25.35 \pm 0.29	20 - 29	1.80	3.24	7.10
E	M	12	19.21 \pm 0.44	17 - 23	1.52	2.31	7.91
	F	13	17.65 \pm 0.46	14 - 21	1.67	2.78	9.46
	T	25	18.40 \pm 0.36	14 - 23	1.78	3.16	10.08
W	M	2	49 \pm 3.54	44 - 54	5	25	10.20
	F	-	-	-	-	-	-
	T	2	49 \pm 3.54	44 - 54	5	25	10.20

specimens examined for tail colour, 25 had white tail tips (ranging from the most distal tail hairs being white, up to 62mm along the tail from the tip) and 27 had uniformly dark tails. White colouring is evident in both tail hair and skin pigment. No specimens west of Telefomin (141°38'E) had white-tipped tails (N=19) while specimens from the east (e.g., Central Morobe Province) showed 24 with white tips and 5 without. One specimen (QM JM6169) from Ofektamin near Telefomin (centre of the *P. naso* range) shows pelage and tail colouration unlike any other specimen. This large adult male has its tail uniformly coloured a dark slate grey with a slightly browner, weak ventral crest. There is no white tip. The mid-back is typically *P. naso* coloured (a dull sepia) but rump and neck are a rich golden brown. It also shows a black stripe passing from the mystaceal vibrissae to the anterior corner of the eye. In cranial and dental features it is indistinguishable from other large *P. naso* specimens.

Size. Largest specimens appear to occur at the east-west extremities of the overall range, with AMNH 1919 from Araboe-bivak (136°26'E) Irian Jaya, measuring BL = 33.72mm and AMNH 221473 from Mt Albert Edward (147°18'E) Papua New Guinea, measuring BL = 33.03mm.

SPECIMENS EXAMINED. Albert Edward Mt., 2257m, 08°22'S 147°18'E (AMNH 221473); Araboe-bivak, 1750m, 03°51'S 136°26'E (RMNH 1919, RMNH 3725); Baiyanka, 2287m, 05°35'S 144°51'E (BMNH 50.1114-50.1116); Bernhard Camp 15km SW, 1500m, 03°32'S 139°10'E (AMNH 152031); Bernhard Camp 15km SW, 1800m, 03°32'S 139°10'E (AMNH 152026-152030); Enarotali, 1765m, 03°56'S 136°13'E (RMNH 520, RMNH 755-756); Enarotali, 1800m, 03°56'S 136°13'E (AMNH 221629, AMNH 222049); Erimbari Mt., 2850m, 06°12'S 145°10'E (QM JM 1095-1096); Gono, 1900m, 06°20'S 145°12'E (AMNH 190875); Habbema Lake 18km N, 2200m, 04°05'S 138°42'E (AMNH 109823, AMNH 151069); Habbema Lake 18km SW, 2150m, 03°33'S 139°09'E (AMNH 152037); Habbema Lake 9km NE, 2800m, 04°05'S 138°50'E (AMNH 109809, AMNH 109814, AMNH 109816-109818); Hellwig Mts, 2000m, 04°32'S 138°41'E (ZM 35134); Kaindi Mt., 1900m, 07°21'S 146°43'E (BBM 54653); Kaindi Mt., 2100m, 07°21'S 146°43'E, (AMNH 190872-190874, BBM 101625, BBM 101640); Kaindi Mt., 2200m, 07°21'S 146°43'E (BBM 105356, BBM 105363, BBM 105369, BBM 105379); Kaindi Mt., 2300m, 07°21'S 146°43'E (BBM 29184, BBM 51029, BBM 53436); Kaindi Mt., 2350m, 07°21'S 146°43'E (BBM 53380); Kamila (Okapa area), 1900m, 06°37'S 145°35'E (AMNH 190877-190879); Kunupi, 1400-1800m, 03°50'S 135°30'E (ZM 91679-91680); Misim Mt., 1900m, 07°13'S 146°50'E (BBM 29088); Misim Mt., 1769m, 07°13'S 146°50'E (MCZ 29923); Misim Mt., 1784m, 07°13'S 146°50'E (MCZ

29924); Moimo, 1830m, 07°59'S 147°01'E (BBM 98044, BBM 98115); Ofektamin, 1500m, 05°12'S 141°38'E (QM JM6169); Paniai, 1750m, 03°55'S 136°23'E (RMNH 518); Shungul Mt., 200m, 06°51'S 146°44'E (BBM 60300); Shungul Mt., 2300m, 06°51'S 146°44'E (BBM 98293); Sonofi (Kainantu area), 1891m, 06°20'S 145°43'E (AMNH 190876); Tafa Mt., 2130m, 08°35'S 147°09'E (AMNH 104040); Tapu, 2287m, 06°14'S 145°50'E (BMNH 50.117-50.1119).

Murexia Tate & Archbold, 1937

Phascogale (in part), Temminck 1824.

Phascologale (in part) Thomas 1888.

TYPE AND ONLY SPECIES. *Phascogale murex* Thomas, 1913 = *longicaudata*. Based on BMNH 12.2.4.1, adult ♂, puppet skin and skull, from Sattelburg, Houn Peninsula, NE PNG, 06°30'S 147°43'E.

GENERIC DIAGNOSIS. M^2 very broad, with wide protocone and complete anterior cingulum, the anterior margin of this tooth is straight or anteriorly convex, but never indented or concave. A relatively unreduced talonid on M_4 with 3 cusps. Tail longer than the head-body length.

It is distinguished from *Phascolosorex* and *Myoictis* by its lack of dorsal body stripes, and from *Neophascogale* by its lack of reduced premolars and lack of a thickly-haired white-tipped tail.

Murexia is immediately separable from *Micro-murexia* by its larger valves for the following measurements (ranges (R) associated with each measurement do not overlap, Table 4); basicranial length BL, zygomatic width ZW, outside bullae width OBW, inside bullae width IBW, rostral widths R-LC¹, R-LM¹, R-LM², R-LM³, maxilla width R-LM¹T, upper tooth row I¹-M⁴, upper premolar row P¹⁻³, upper molar row M¹⁻⁴, upper second molar width M²W, lower tooth row I₁-M₄, lower premolar row P₁₋₃, lower molar row M₁₋₄, lower second molar width M₂W, total length TL and hind foot HF.

Murexia is separable from *Phascomurexia* by the longer lower tooth row I₁-M₄.

Murexia is separable from *Murexechinus* by the longer upper and lower premolar rows P₁₋₃.

Murexia is separable from *Paramurexia* by its lack of a black, longitudinal head-body stripe and accompanying black facial mask.

Murexia longicaudata (Schlegel, 1866)

(Figs 21, 22)

Phascogale longicaudata Schlegel, 1866: 356.

Phascogale murex Thomas, 1913: 80.

Phascogale murex aspera Thomas, 1913: 211.

Phascogale maxima Stein, 1932: 254.

HOLOTYPE. RMNH 35135, subadult ♂, very old, faded mount and skull extracted (skin faded, skull deformed with basioccipital region missing).

TYPE LOCALITY. Wonoembai, Aru Islands, Irian Jaya 6°00'S 134°30'E. <100m. Coll. M. von Rosenberg, 1865.

DIAGNOSIS. As for genus.

DESCRIPTION. HOLOTYPE. *Pelage* (Fig. 21) faded; head shows insect damage, and patches of fur are missing from the body. The head appears as a Tawny Olive, mid-back and shoulders appear as Sepia and rump in a warm Sepia.

Fur of the mid-back (4.3mm long) has basal 3.3mm Slate colour, median 0.6mm Cinnamon Buff and apical 0.4mm Fuscous Black. Sepia guard hairs are thickly interspersed through the fur and are 3.6mm on the head, 7.5mm on the mid-back and 9.0mm on the rump. Fur of the head is 2.17mm long with similarly pigmented basal, median and apical bands which are 2.11 mm, 0.3mm and 0.3mm respectively. Fur of the rump is 7.03mm long with similarly pigmented basal, median and apical bands 4.7mm, 1.62mm and 0.71mm respectively, however the median band is coloured Mikado Brown.

The head lacks a stripe and there is no head patch or eye-ring. The ventral fur (5mm long on the belly and interramal region) is Deep Olive Buff (a 'dirty' off-gray) on the basal half and Warm Buff on the apical half and is interspersed with Cream-Buff guard hairs 6.4mm long. The belly is thus an overall Warm Buff. Forefeet are thinly covered with Sepia coloured hairs and hindfeet are similarly coloured. The tail is weakly bicoloured with dorsal hairs averaging 1.3mm and ventral hairs averaging 1.8mm along its length until the tip where hair length increases to 3.3mm dorsally and 4.7mm ventrally. Dorsal hairs appear a dark Clove Brown — this results from a combination of black guard hairs and Mikado Brown guard hairs. Ventrally the hairs are all the same colour, Burnt Umber.

Vibrissae. Approximately 9 mystaceal vibrissae occur on the left side and 14 occur on the right. The more dorsal of these are coloured a faded Sepia with those more ventral are colourless; supra-orbital vibrissae (Sepia) number 2 (left) and 2 (right); genals (Sepia and colourless) number 0 (left) and 9 (right), ulna-carpals (colourless) number 4 (right) and 0 (left); submentals (colourless) number 4.

Tail. Tail very long (much longer than the head and body), thin, tapering toward the tip.

Hindfoot. Interdigital pads separate. The apical granule is enlarged, elongate and striate. Hallucal and post-hallucal pads are long and fused. Metatarsal pads are long, narrow and striate.

Ears. Pinnae are large with a complex supratragus which has a pronounced thickened posterior margin and the distal end is reflected ventrally. The reflected tip is (presumably in the mount) concave.

Dentition (Fig. 22). Upper Incisors: I^1 is narrow, procumbent and slightly curved, taller crowned than all the other incisors and separated by a diastema from I^2 . Left and right I^1 are just separate. In crown heights $I^1 > I^3 > I^2$. All upper incisors lack buccal cingula yet there is no lack of differentiation between root and crown. I^1 carries no anterior or posterior cusps. The roots of I^1 are narrow. The premaxillae of the holotype are grossly deformed having folded lingually and being also reflected posteriorly so that all right incisor crowns orient toward all left incisor crowns, and all crowns orient posteriorly.

Upper Canines: C^1 is slender, very long and caniniform with an indistinct boundary between root and crown. There are no buccal or lingual cingula, and no anterior or posterior cusps. Both R and LC^1 appear not to have erupted fully and are both abnormally deflected lingually. Long, deep grooves occur obliquely between I^4 and the lingual edge of C^1 where C^1 has occluded.

Upper Premolars: Premolars are abnormally square and crushed. In crown height $P^3 > P^2 > P^1$. All upper premolars carry strong buccal and weak lingual cingula. Small anterior and posterior cusps occur on all premolars. P^1 and P^2 possess postero-buccal lobes and P^3 does not contact M^1 .

Upper Molars: The posterior tip of P^3 is not in the parastylar corner of M^1 but lingual to and well below stylar cusp A. The anterior cingulum below stylar cusp B is short, broad and complete. Stylar cusp B and the paracone are relatively unworn and no protoconule is present at the base of the paracone apex. The paracone on M^1 is approximately half the height of the metacone. Stylar cusp C is very well developed on LM^1 and RM^1 , and stylar cusp E is visible. M^1 possesses a posterior cingulum.

In M^2 the broad, complete anterior cingulum which contacts the metastylar corner of M^1 , tapers quickly as it progresses down and along the base of the paracrista and finally unites with the trigon basin of the paracone apex. No protoconule is visible. M^2 has a prominent stylar

cuspid A, a small C and a just visible stylar cusp E. Stylar cusp D is robust and broad and there is a posterior cingulum.

In M^3 the anterior cingulum is as broad and long as in M^2 . It is complete. Stylar cusp D is reduced to a very small, dense peak. Stylar cusp E is present, but stylar cusp C is not. A posterior cingulum is present.

In M^4 the metastylar corner is well developed. The anterior cingulum is complete and a posterior cingulum is also present. The protocone is reduced but broad. In occlusal view the angle made between the post-paracrista and the post-protocrista is close to 120° . There is slight development of the metacone.

Lower Incisors: The lower incisor row is abnormally crowded and the incisors crushed. LI_1 folds over, and anterior to RI_1 . A supernumary incisor with degenerate I_1 morphology is fully erupted posterior to LI_1 . The first lower incisor is slightly larger in crown height than I_2 . I_1 and I_2 are oval in anterolateral view and gouge-like in occlusal view. I_2 is sub-equal in crown height to I_3 . I_3 is slightly premolariform in lateral view with a conspicuous posterior cusp at the base of a crest which descends posteriorly from the apex of the primary cusp. The lower canine rests against this posterior cusp. In occlusal view, a small notch separates the posterior cusp from the prominent posterolingual lobe, and the crown enamel of the primary and posterior cusps folds noticeably lingually such that the crest of the two cusps bisects the tooth longitudinally.

Lower Canines: C_1 is caniniform, with forward and erect projection and maximal curvature from root to crown tip. It has weak buccal and lingual cingulation and no posterior cusp. The dentary is abnormally widened below the premolars and canines.

Lower Premolars: P_{1-2} are abnormally crushed into each other and on to C_1 . All are weakly cingulated buccally and lingually. In crown height $P_2 > P_3 > P_1$. P_1 and P_2 are abnormally broad and massive and P_3 is oblique to the dentary thereby avoiding contact with P_2 . All possess weak cingular cusps and none possess anterior cusps. The bulk of each premolar mass is concentrated posterior to the line drawn transversely through the middle of the two premolar roots. Postero-lingual and postero-buccal lobes are featured in P_1 and P_2 .

Lower Molars: All molars are narrow. The M_1 talonid is wider than the trigonid and the anterior cingulum is present but poorly developed. It

continues into a weak buccal cingulum. The paraconid is greatly reduced and appears in occlusal view as a small steeply-sided spur, the lingual edge of which makes a slight swelling on the endoloph of M_1 . The paracristid is scarcely detectable from paraconid to paracristid fissure and is approximately 45° from the paracristid fissure to the protoconid. The metacristid is roughly oblique to the long axis of the dentary and the hypocristid is also oblique. The cristid obliqua is long and extends from the hypoconid to the posterior wall of the trigonid intersecting the trigonid at a point slightly lingual to that point directly below the tip of protoconid. The hypocristid extends from the tip of the hypoconid to the metastylid. The entoconid is low. From the base of the metaconid posteriorly, the talonid endoloph follows the line of the dentary until the base of the hypoconulid. In M_2 the trigonid is slightly narrower than the talonid. The anterior cingulum is very well developed and continues into a weak buccal cingulum which is slightly broken at the base of the protoconid. A strong posterior cingulum extends from the hypoconulid to the posterior base of the hypoconid and anteriorly to the weak buccal cingulum. The paraconid is well developed and is the smallest trigonid cusp. The metastylid and minute entoconid are subequal in height but are both very poorly developed. The cristid obliqua extends from the hypoconulid to the posterior wall of the trigonid, intersecting the trigonid at a point directly below the tip of protoconid but well buccal to the metacristid fissure. The hypocristid extends from the hypoconulid tip to the tip of hypoconid. From the base of the metaconid posteriorly, the endoloph follows a line buccal to that of a dentary axis.

In M_3 the trigonid is wider than the talonid. An indistinct parastylid wraps around the hypoconulid of M_2 and there is a weak anterior cingulum on M_3 . Buccal and posterior cingula are as in M_2 but more poorly developed. The cristid obliqua intersects the trigonid at a point well lingual to the longitudinal vertical midline drawn through the tip of the protoconid, but slightly buccal to the metacristid fissure. There is a poorly developed entoconid on M_3 . The endoloph on the talonid of M_3 takes a more buccal orientation than that seen in M_2 . The rest of M_3 morphology is as in M_2 except that a small crest runs down from the hypoconulid to the origin of the hypocristid.

In M_4 the trigonid is wider than the talonid. The anterior cingulum is stronger than in M_2 . Posterior and buccal cingula are weak. Of the

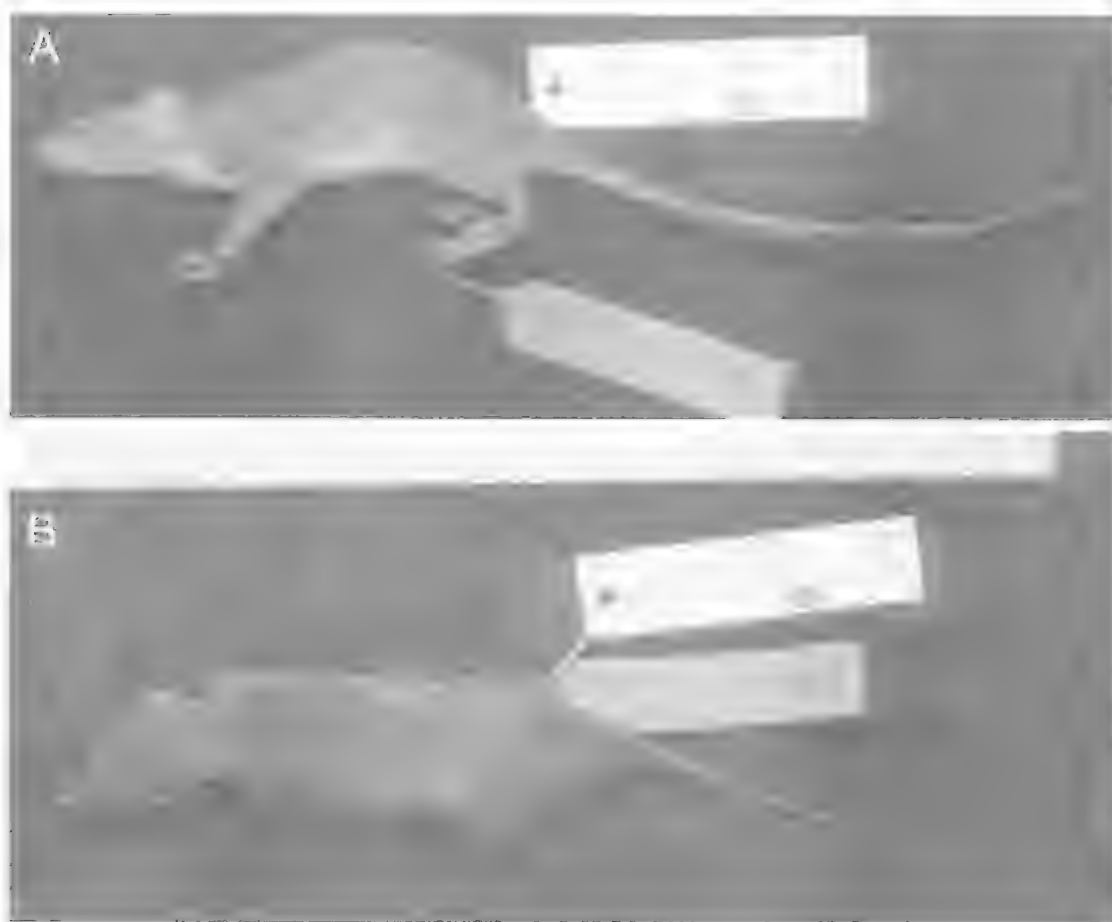


FIG. 21. Holotype of *Phascogale longicaudata* Schlegel, 1866 (= *Murexia longicaudata*). RMNH 35135, study skin; A, lateral view; B, dorsal view. Only external measurement available TL = 324mm; T = 175mm.

three main trigonid cusps, the metaconid is slightly taller than the paraconid but both are dwarfed by the protoconid. The hypoconid of the M_4 talonid is much more reduced than in M_3 . Between the hypoconid and the base of the metacristid, the cristid obliqua forms a low, weak crest which meets the trigonid lingual to the metacristid fissure. A significant feature of M_4 morphology is the retention of a broad buccal cingulum. The hypoconid is well formed as is the hypoconulid. The entoconid is represented by a barely discernible bump of enamel.

Skull (Fig. 22). The basicranium is missing from the holotype from the level of the entocarotid foramina posteriorly. The nasals are minimally inflated, creating a slight depression at the nasal-frontal suture in the interorbital region. The premaxillary vacuities extend from the level of the I^2 root back to midway along the C^1 root. The

very small maxillary vacuities extend from the level of the metacone root of M^1 and extend back to the level of the protocone root of M^3 . Palatine vacuities are absent.

SYNONYMS

Phascogale murex Thomas, 1913
(Figs 23, 24)

HOLOTYPE. BMNH 12.2.4.1, adult ♂ puppet skin with skull extracted (skin in good condition, basicranium posterior to alisphenoid bullae, missing).

TYPE LOCALITY. Sattelburg, Huon Peninsula, NE PNG, 06°30'S 147°43'E. At 290m. Coll. O. Fritsche.

P. murex differs from the *longicaudata* holotype in the following respects.

Pelage (Fig. 23). The skin appears as a uniform Sepia. It has a well-developed, ventral tail crest.



FIG. 22. Holotype of *Phascogale longicaudata* Schlegel, 1866, RMNH 35135, cranium and dentary. Sex ♀, m; BL = -; ZW = 20.97; IO = 7.30; OBW = 12.69; IBW = 5.66; R-LC¹ = 6.88; R-LM¹ = 12.22; R-LM² = 14.88; R-LM³ = 17.44; R-LM¹T = -; M²W = 2.37; I¹-M⁴ = 20.46; P¹⁻³ = 4.29; M¹⁻⁴ = 9.40; Dent = 27.39; I₁-M₄ = 15.87; P₁₋₃ = 4.29; M₁₋₄ = 9.40; M₂W = 1.56.

Dentition (Fig. 24). RP³, RM¹, RM³ and RI¹ are missing; . Despite the deformity of the holotype of *longicaudata*, *murex* exhibits a similar incisor gradient with I¹ procumbent and I⁴ > I³ > I². I¹ is very narrow and slightly built.

Upper Canines: C¹ is long, slender, fully erupted and displays no abnormal, oblique, lingual deflection as noted in the *longicaudata* holotype.

Upper Premolars: The premolars are narrow, elongate, and widely spaced. C¹ and P¹, and P³ and M¹ are in close juxtaposition. A diastema

occurs between P² and P³, but this is smaller than the large diastema which separates P² and P³. Postero-lingual lobing is not featured in any of the upper premolars. In crown height P³ is much greater than P² which is greater than P¹.

P¹ and P² are minute premolars, and P³ is characterised by a long exposed anterior root. All premolars possess strong buccal cingula. P¹ and P² have both anterior and posterior cingular cusps. P³ lacks an anterior cusp but possesses a small posterior cusp.

Upper Molars: The posterior tip of P^3 lies in the parastylar corner of M^1 and is lingual to and just below stylar cusp A. Stylar cusp B is very large but C is absent. In M^2 stylar cusps C and E are absent.

In M^3 stylar cusps C and E are just visible. In M^4 there is a great reduction in the length of the paracone which is broad, but very short. There is no development of the metacone.

Lower Incisors: There is no crushing among the lower incisors as in the *longicaudata* holotype. I_1 is much larger than I_2 or I_3 . Only 3 right and 3 left incisors are present (i.e., the normal condition).

Lower Canines: C_1 is bulky and strongly curved.

Lower Premolars: The lower premolar row is uncrowded although C_1 and P_1 are closely juxtaposed. A large diastema occurs between P_2 and P_3 . All premolars are narrow and elongate with no evidence of posterolingual lobing. In crown height $P_3 > P_2 > P_1$ and all possess buccal and lingual cingula.

Lower Molars: In M_1 the paraconid is very well developed. Anterior and buccal cingula are very strongly developed as is the entoconid.

M_2 has a well developed paraconid, strong buccal and anterior cingulation and a large entoconid. The trigonid is narrower than the talonid.

In M_3 the trigonid is wider than the talonid. The anterior, buccal and posterior cingula are complete, and the entoconid is large.

In M_4 all 3 talonid cusps are well developed. The hypoconid is larger than the entoconid which is larger than the hypoconulid.

Skull (Fig. 24). The premaxillary vacuity (4.32mm long) extends from the level of the I^1 root back to the level of middle of the C^1 root. The maxillary vacuities (3.31mm long) extend from the level of the M^1 protocone root back to the level of the M^2 metacone root.

Phascogale murex aspera Thomas, 1913
(Figs 25, 26)

HOLOTYPE. BMNH 13.6.18.90. Adult ♀ puppet skin with skull extracted (skin and skull in good condition).

TYPE LOCALITY. Utaqua River, Camp No. 3, Irian Jaya, 04°24'S 137°12'E. At 762m. Coll. C.B. Kloss, 1 December 1912.

P. murex aspera differs from the *longicaudata* holotype in the following respects (apart from the abnormalities).

Dentition (Fig. 26). As for *P. longicaudata* except C^1 is relatively small (always relatively

smaller in ♀♀). The only diastema in the upper premolar row occurs between P^1 and P^2 . Buccal cingula occur only on P^2 and P^3 , weak lingual cingula occur on P^2 and P^3 . On M^1 and M^2 stylar cusp C is large and stylar cusp E is very large. The anterior and posterior cingula are broad and complete. In M^3 anterior and posterior cingula are well developed, stylar cusps C and E are present and D is greatly reduced.

Lower Premolars: Premolars are tightly arranged though there is no crowding of the premolar row. In the left dentary the diastema separating P_1 and P_2 is greater than that which separates C_1 and P_1 . In the right dentary these diastemata are equal. In crown size P_2 is slightly longer than P_1 , but in crown height P_3 is taller than the other 2 premolars.

Lower Molars: The M_1 paraconid is moderately well developed and the entoconid is large. The M_3 trigonid is smaller than the talonid, the entoconid is large but it does not contribute to the bulk of the endoloph between metaconid and hypoconulid. In M_4 the cingulation is reduced (compared to that of M_3). The talonid shows moderate development of the three talonid cusps, with the hypoconid larger than the well developed hypoconulid which is larger than the small entoconid.

Skull (Fig. 26). The premaxillary vacuity (4.14mm long) extends from the level of the M^1 root to the posterior end of the C^1 root. The maxillary vacuities (3.01mm long) extend from the level of the M^2 protocone root back to the protocone root of M^3 .

Phascogale maxima Stein, 1932
(Figs 27, 28)

HOLOTYPE. ZM 44228. Very large adult ♂ puppet skin with skull extracted (skin and skull in excellent condition).

TYPE LOCALITY. Yapen Island, Geelvink Bay, W Irian Jaya, 01°45'S 136°10'E. At 50m. Coll. G. Stein, 18 March 1931.

P. maxima differs from the *longicaudata* holotype in the following respects.

Pelage (Fig. 27). Head, back rump and the dorsal surface of the tail are coloured Saccardo's Umber. Sides of the body are Clay coloured and the belly is an Olive Buff. The tail is practically naked. There are approximately 20 left and 15 right mystacial vibrissae of which the longest are 30mm. The more dorsal are coloured Fuscous Black while those lower are colourless; supra-orbital vibrissae (Fuscous Black) number 1 (left)

and 0 (right); genals (Fuscous Black and colourless) number 8 (left) and 12 (right); ulna-carpals (colourless) number 2 each side; submentals (colourless) number 4. The fur has a very spinous texture and is difficult to rub against (from rump to head).

Dentition (Fig. 28). Upper Incisors: I^1 is narrow with the tips curved posteriorly. Left and right I^1 are just separate.

Upper Canines: C^1 is moderately broad but exceptionally long.

Upper Premolars: All premolars are narrow, elongate and widely spaced. The diastema separating P^2 and P^3 is greater than that separating P^1 and P^2 which is greater than that between the canine and P^1 . In crown height $P^3 > P^2 > P^1$. Small anterior and posterior cingular cusps on P^1 and P^2 , but not P^3 .

Upper Molars: The posterior tip of P^3 is just buccal to the parastylar corner of M^1 . The anterior cingulum below stylar cusp B is short, broad and incomplete. In M^2 the broad anterior cingulum tapers quickly as it progresses down and along the base of the paracrista and finally degenerates mid-way along the paracrista. LM^2 shows stylar cusps A and C while RM^2 shows A and E. In M^3 the anterior cingulum is as in M^2 but degenerates soon after it leaves the parastylar corner. Stylar cusp C is not present in M^3 . In M^4 the metastylar corner is well developed (but much more indistinct than that seen in *Phascosorex*). A posterior cingulum is absent.

Lower Incisors: LI_{1-3} missing; RI_1 is deformed.

Lower Premolars: The lower premolar row is very long and uncrowded. Diastemata (arranged in decreasing length) occur between P_2 and P_3 , P_3 and M_1 , P_1 and P_2 , C_1 and P_1 . In crown height $P_3 > P_2 > P_1$. All premolars are narrow and elliptical in occlusal view. All possess weak posterior cusps. There is no posterolingual lobing.

Lower Molars: In M_1 the paraconid is greatly reduced. In M_2 the anterior cingulum is very poorly developed. In M_3 the entoconid is well developed but does not contribute bulk to the endoloph between the metacone and the hypoconulid. In M_4 the anterior cingulum is stronger than that seen in M_2 . A posterior cingulum is absent. The hypoconulid is the strongest M_4 cusp, while the hypoconulid and entoconid are small.

Skull (Fig. 28). The nasals are raised, slightly fluted and form a smooth semi-circular rostrum with a conspicuous concavity at the junction of the nasal and frontal bones just anterior to the anterolateral region. The interorbital width is

very narrow. The right and left alisphenoid tympanic bullae are minute and widely separated. The foramina pseudovale are very large and open, the eustachian canal opening large and the posterior lacerate foramina are very small. The premaxillary vacuities extend from the level of the I^2 root back to the anterior of the C^1 root. The maxillary vacuities extend from the level of the protocone root of M^1 back to the level of the M^3 protocone root. Palatine vacuities are absent.

ADDITIONAL DIAGNOSTIC FEATURES

Murexia longicaudata differs from all other dasyurids in the combination of the following features: 1, widely spaced R and LI^1 that are needle-like and only slightly procumbent, extremely thin, and with a spur-like crown; 2, an uncingulated upper incisor row where $I^2 < I^3 < I^4$; 3, extremely long, relatively thin, needle-like upper canines in which the root and crown are undifferentiated, and in which there is no posterior cusp; 4, an upper premolar row in which the lightly cingulated teeth are uncrowded, narrow and without postero-lingual lobing; 5, a P^3 , the anterior root of which, in larger individuals, elongates to the extent that P^3 is lowered into the upper molar plane where it acts as an increment to the molar row. Here the P^3 crown and much of the anterior root act as a sheering crest against the greatly enlarged primary cusp of the P_3 ; 6, M^1 very broad, with wide protocone and complete anterior cingulum, the anterior margin of this tooth is straight or anteriorly convex, but not indented or concave; 7, M^1 and M^2 stylar cusp B large (slightly smaller than stylar cusp D in M^1 , subequal in M^2); 8, M^4 protocone more narrow than in *Micromurexia* and *Phascomurexia* but anterior cingulum complete; 9, M^1 and M^2 stylar cusp D a relatively low crest rather than a tall cone; 10, M^4 metacone relatively large; 11, a poorly cingulated lower premolar row in which the narrow teeth are very widely spaced and where P_3 is larger than P_2 ; 12, cingulated P_3 ; 13, M_3 talonid narrower than trigonid; 14, well-developed paraconid on M_1 ; 15, three poorly developed cusps on the M_4 talonid; 16, tall entoconid on M_2 ; 17, metacristids and hypocristids are not transverse to the long axis of the dentary; 18, skull elongate, domed in smaller individuals but flat in the very large; 19, fluted nasals; 20, poorly developed tympanic wing of the alisphenoid with no contrasting expansion of the pars mastoidea and adjacent squamosal; 21, variable presence of a single post-metatarsal pad and calcaneal pad on hind

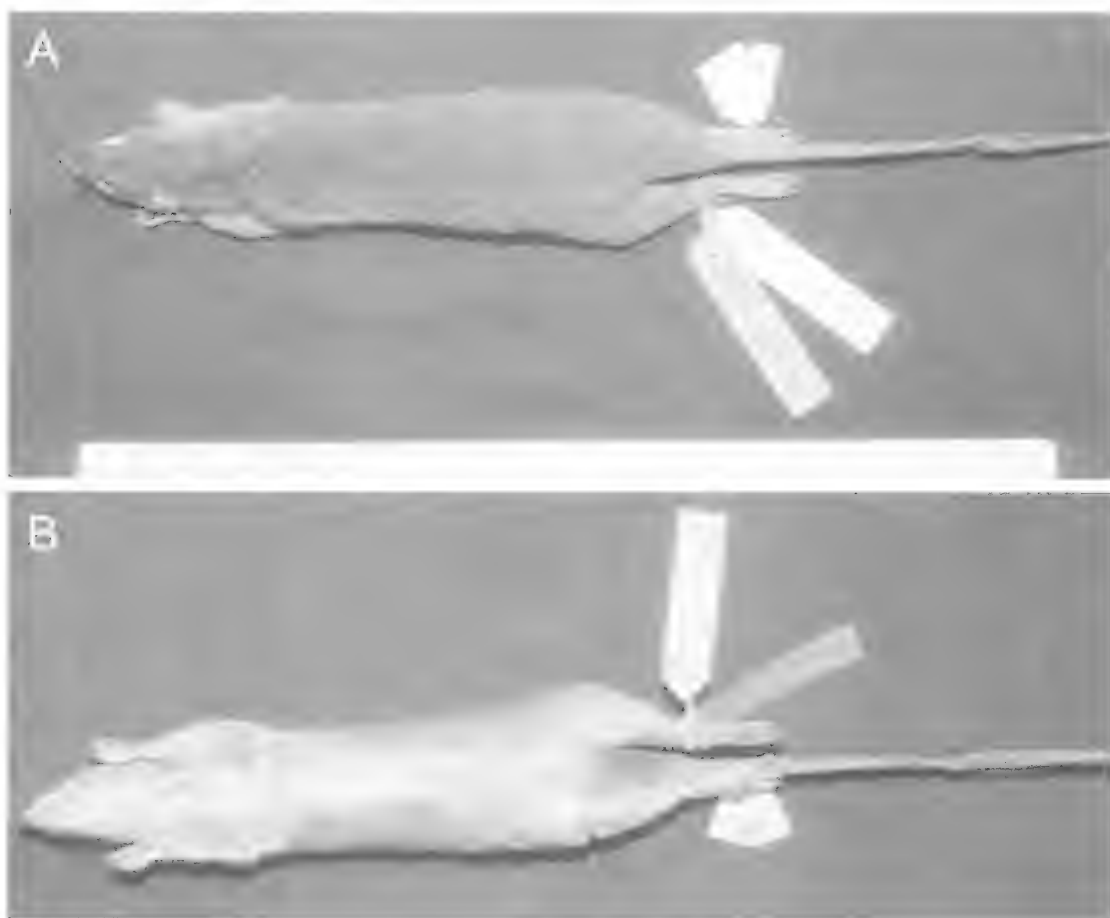


FIG. 23. Holotype of *Phascogale murex* Thomas, 1913 (= *Murexia longicaudata*). BMNH 12.2.4.1, study skin; A, dorsal view; ventral view. TL = 457mm; HB = 222mm; TV = 235mm; HF = 41mm.

foot; 22, tail almost naked brown with very weak ventral crest developing toward distal tip, the tail being generally longer than the head-body length; 23, polyoestrous and nipple number low (4); 24, penile morphology is simple; 25, body size can be large.

In addition to the features noted in the generic diagnosis *M. longicaudata* differs significantly ($P < 0.001$) from *Mi. habbema* as follows (measurements are means, mm): longer dentary Dent (36.17:21.46); longer tail T (197:135); longer ear E (20.50: 16.95); strong thick claws rather than semi-straight slender claws; tail almost naked dorsally rather than well-haired; short, harsh fur rather than long silky fur.

M. longicaudata also differs significantly ($P < 0.001$) from *P. naso* as follows: longer basicranial BL (43.64: 30.13); broader zygomatic

width ZW (25.33: 17.45); broader basicranium measured outside bullae OBW (14.59: 11.57); broader inside bullae IBW (8.44: 5.81); wider rostrum at R-LC¹ (8.40: 5.91); R-LM¹ (14.71: 10.57), R-LM² (17.80: 12.97), R-LM³ (21.24: 15.48); broader maxilla R-LM¹T (11.95: 8.50); longer upper tooth row I¹-M⁴ (25.01: 17.32), longer upper premolar row P¹⁻³ (7.49: 4.63); longer upper molar row M¹⁻⁴ (10.10: 7.61); wider upper second molar M²W (2.75: 2.02); longer dentary Dent (36.17: 24.23); longer lower molar row M₁₋₄ (10.90: 8.32); longer lower tooth row I₁-M₄ (22.73: 15.18); longer lower premolar row P₁₋₃ (7.92: 4.73); wider lower second molar M₂W (1.71: 1.31); longer total length TL (398: 275); longer tail T (197: 149); longer hind foot HF (35.22: 25.35); longer ear E (20.50: 18.40); fur short and harsh rather than long and luxurious; ventral tail-tip with poorly developed crest rather

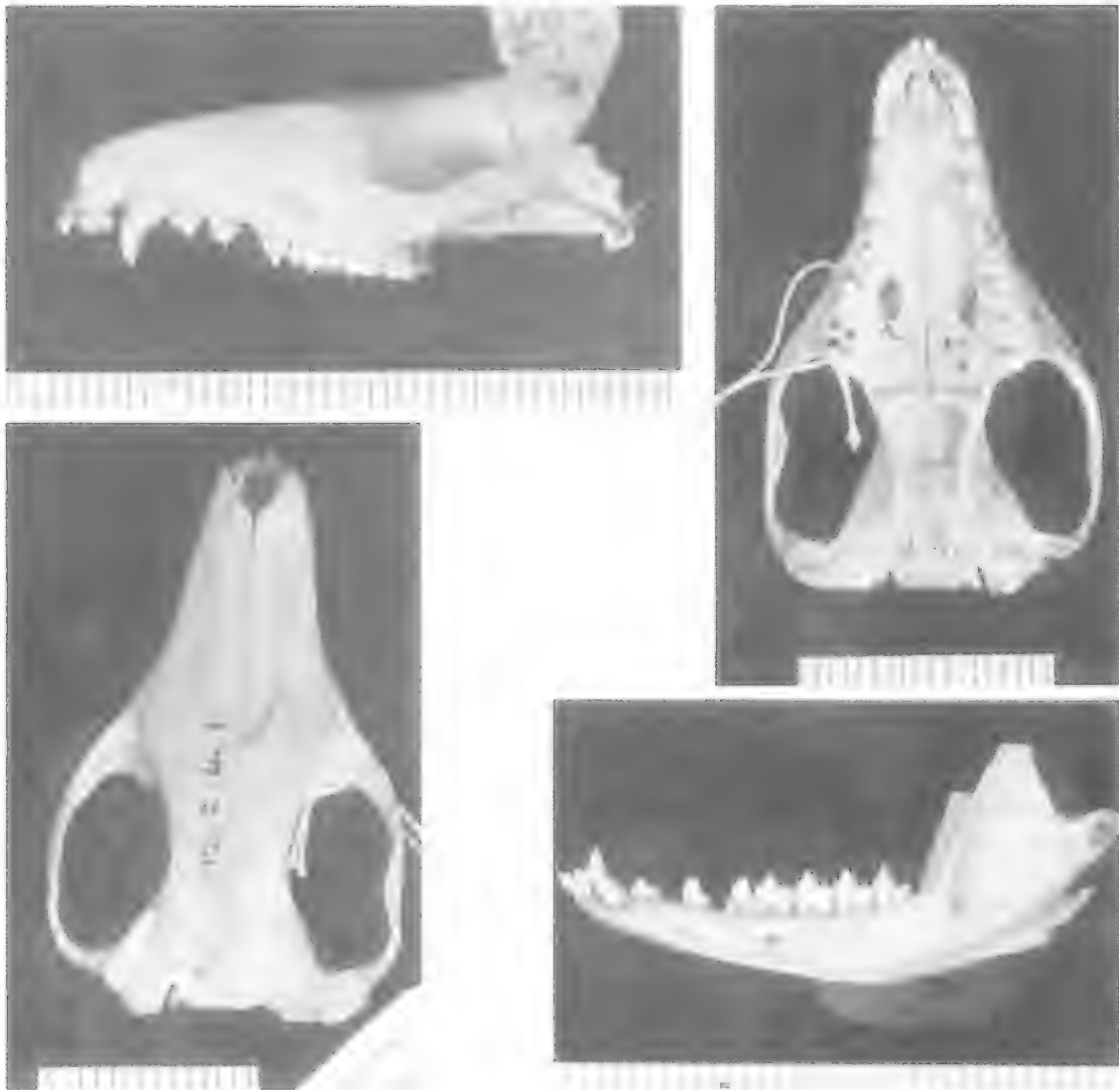


FIG. 24. Holotype of *Phascogale murex* Thomas, 1913, BMNH 12.2.4.1, cranium and dentary. Sex = m; BL = -; ZW = 23.84; IO = 7.71; OBW = -; IBW = 7.01; R-LC¹ = 8.12; R-LM¹ = 15.26; R-LM² = 17.94 R-LM³ = 21.01; R-LM¹T = 11.45 M¹W = 2.58; I¹-M⁴ = 24.12; P¹⁻³ = 7.85; M¹⁻⁴ = 9.08; Dent = 36.08; I₁-M₄ = 21.47; P₁₋₃ = 8.23; M₁₋₄ = 10.03; M₂W = 1.54.

than well developed crest; left and right upper first incisors separate rather than in contact.

M. longicaudata differs significantly ($P < 0.001$) from *Murexechinus melanurus* as follows: longer basicranium BL (43.64: 26.83); broader zygomatic width ZW (25.33: 16.89); broader interorbital IOW (7.81: 7.09); broader outside bullae OBW (14.59: 10.99); broader inside bullae IBW (8.44: 5.12); wider rostrum at R-LC¹ (8.40: 5.43), R-LM¹ (14.71: 9.71), R-LM² (17.8: 11.91), R-LM³ (21.24: 14.12); wider

maxillae at R-LM¹T (11.95: 7.69); longer upper tooth row I¹-M⁴ (25.01: 14.88); longer upper premolar row P¹⁻³ (7.49: 3.37); longer upper molar row M¹⁻⁴ (10.10: 6.78); wider upper second molar M² (2.75: 1.89); longer dentary DL (36.17: 21.31); longer lower tooth row I₁-M₄ (22.73: 12.96); longer lower premolar row P₁₋₃ (7.92: 3.45); longer lower molar row M₁₋₄ (10.90: 7.37); wider lower second molar M₂W (1.71: 1.22); longer total length TL (398: 247); longer tail T (197: 133); longer hind foot HF (35.22: 22.27);

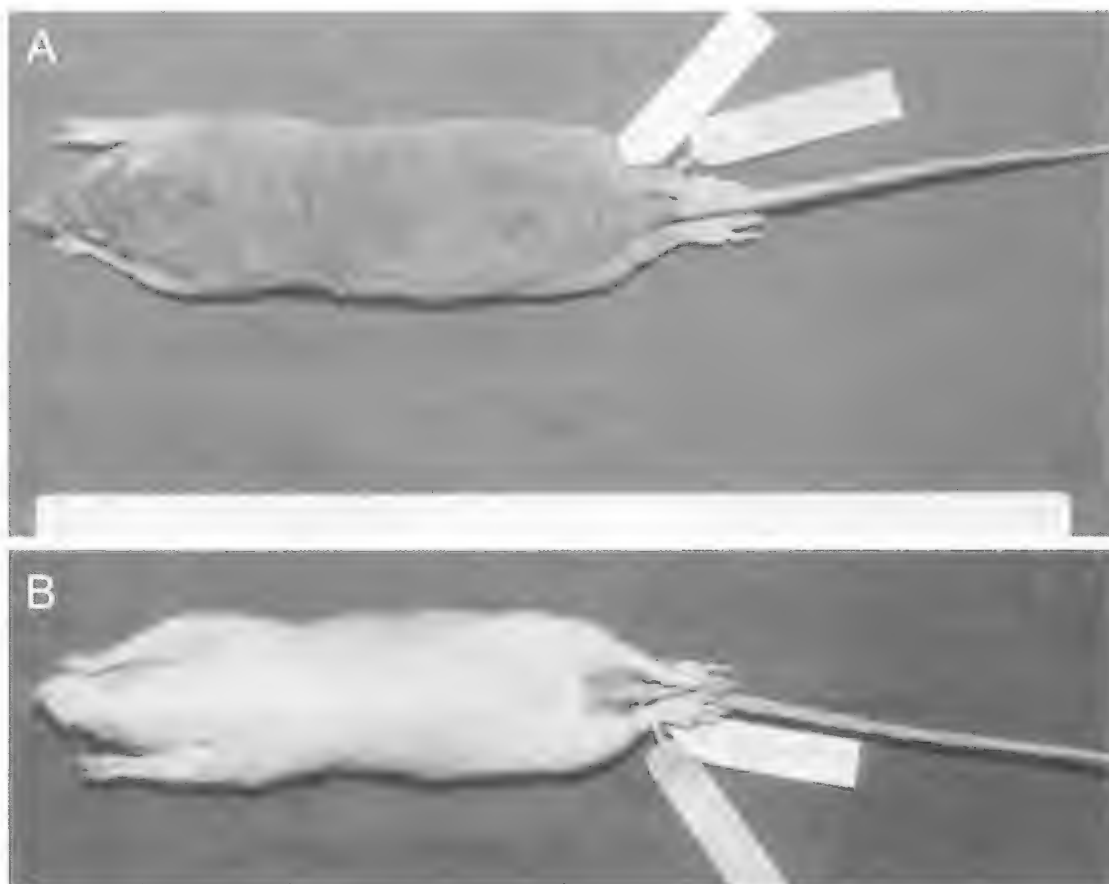


FIG. 25. Holotype of *Phascogale murex aspera* Thomas, 1913 (= *Murexia longicaudata*). BMNH 13.6.18.90, study skin; A, dorsal view; B, ventral view. TL = 349mm; HB = 169mm; TV = 180mm; HF = 33mm.

longer ear E (20.50: 15.83), ears always lack rufous post-auricular patches rather than ears always with patches; pelage uniform brown throughout rather than a definite colour change from agouti to warmer russet; pelage harsh, short and spinous throughout rather than fur long and soft; tail almost naked brown with very weak ventral crest developing toward distal tip rather than tail thickly-haired a uniform black (sometimes dark brown) with ventral crest hairs long throughout entire length; I^1 narrow and needle-like rather than broad and claw-like, $I^4 > I^3 > I^1$ rather than $I^2 \geq I^3 \geq I^4$; $C^{1/1}$ very long and slender rather than short and thick; premolar row with uncrowded, narrow and widely spaced premolars rather than premolar row short with premolars crowded and broad; rostrum elongate rather than short and broad; nasals fluted rather than the nasals flatter.

M. longicaudata differs significantly ($P < 0.001$) from *Paramurexia rothschildi* as follows: broader skull at R-LM² (17.80: 14.79) and R-LM³ (21.24: 17.65); longer upper tooth row I^1 -M⁴ (25.01: 19.68); longer upper premolar row P^{1-3} (7.49: 4.77); longer upper molar row M^{1-4} (10.10: 8.71); longer lower premolar row P_{1-3} (7.92: 4.07); I^1 long, narrow and needle-like rather than broad and claw-like; premolar row with uncrowded, narrow and widely spaced premolars rather than premolar row short with premolars crowded and broad; P^4 three-rooted rather than single-rooted; M^4 with metacone rather than without metacone; M_4 with entoconid rather than without; hind foot lacks specialisations such as large striate auxillary pad outside the third interdigital pad, greatly elongate metatarsal pad which almost contacts the third interdigital pad and highly developed, striate post-metatarsal and calcaneal pads.

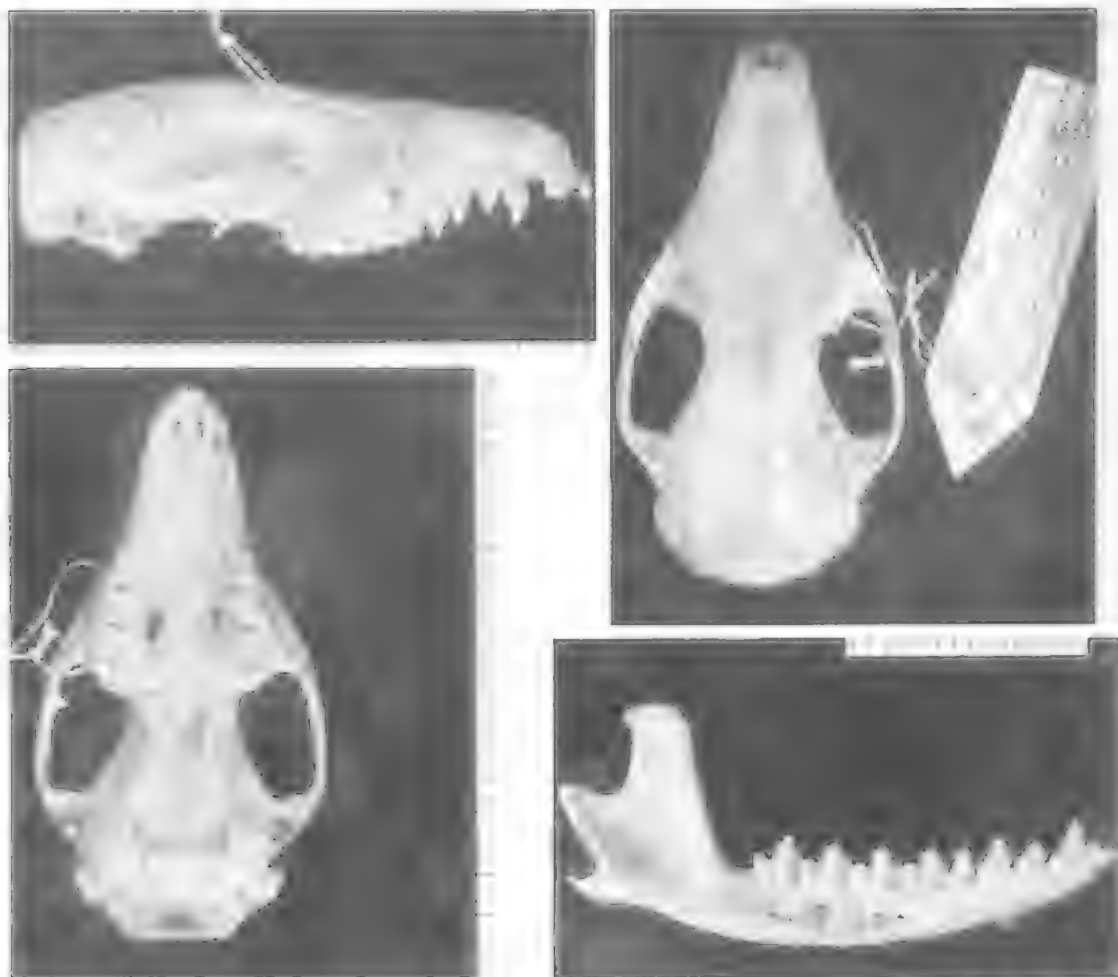


FIG 26. Holotype of *Phascogale murex aspera* Thomas, 1913. BMNH 13.6.18.90, cranium and dentary. Sex = f; BL = 39.96; ZW = 23.01; IO = 8.69; OBW = 14.31; IBW = 7.37; R-LC¹ = 8.13; R-LM¹ = 14.19; R-LM² = 17.63; R-LM³ = 20.34; R-LM¹⁺² = 11.01; M²W = 2.78; I¹-M⁴ = 23.22; P¹⁻³ = 6.33; M¹⁻⁴ = 10.37; Dent = 32.39; I₁-M₄ = 20.84; P₁₋₃ = 6.24; M₁₋₄ = 11.27; M₂W = 1.90.

REMARKS. *Taxonomic History.* The distinctive appearance of *Murexia longicaudata* has assured it of a relatively stable taxonomic history at the generic level notwithstanding firstly, its unflattering introduction to Science, 'Cette espèce rapelle, par sa taille, le jeune du rat ordinaire' (Schlegel, 1866:356) and secondly, the multiple deformities associated with the holotype skull (premaxillaries, upper and lower incisors, canines, premolars and the dentary). The species' extraordinary range in body size, however, has brought with it an array of described forms.

Although immature, the holotype is a very small male and would have matured to a small adult. This is reflected in the following

measurements (in mm): M¹⁻⁴ = 8.5, M₁₋₄ = 9.4, M² width = 2.37, M₂ width = 1.56. The only specimens examined which approach this diminutive size are some very small individuals from the Kratke Mountains (at 8,000m) e.g., BMNH 50.1403, BMNH 50.1404, BMNH 50.1405. This locality occurs on virtually the same latitude (6°S) as Aru Islands but is situated approximately 1300 km to the east).

Thomas (1913) described *murex* on the basis of its large size, 'This fine *Phascogale* is readily distinguished by its greater size from its only near ally *Ph. longicaudata*, Schleg., a native of the Aru Islands' (p. 80). The external measurements accompanying Thomas' description appear to

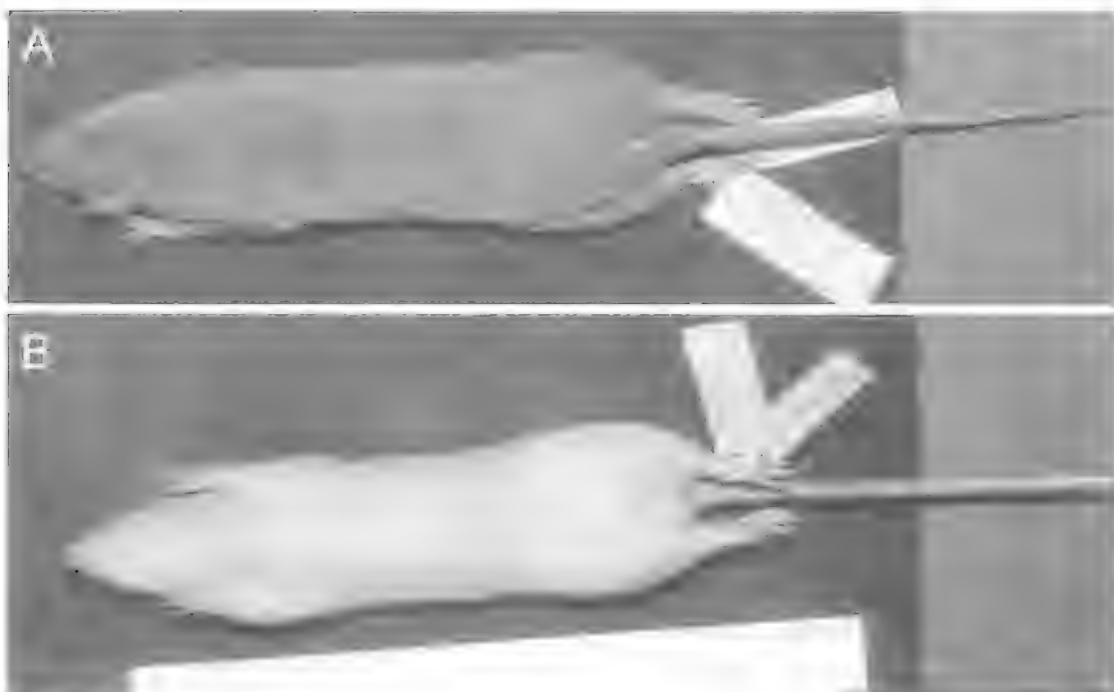


FIG. 27. Holotype of *Phascogale maxima* Stein, 1932 (= *Murexia longicaudata*). ZM 44228, study skin; A, dorsal view; B, ventral view. TL = 450mm; 'head-rump' = 235mm; 'tail' = 215mm; HF = 40mm.

support this claim, yet an examination of the type specimen reveals an obvious error with Thomas' measurements. He quotes 'Head and body 197mm; tail 167 ...' (p. 80) but these are not borne out in the skin which has a tail length much greater than its head and body length (in keeping with other intact *Murexia* examined). Thomas may have inadvertently translocated the two measurements, but his *murex* male is, nevertheless, a small animal ($M^{1-4} = 9.08$, $M_{1-4} = 10.03$, M^2 width = 2.58, M_2 width = 1.54mm) not appreciably larger than the Leiden *P. longicaudata* holotype.

A few months later, it might have been with some misgivings that Thomas assessed the significance of a newly collected specimen presented to him by G.B. Kloss of the 1912 Wollaston Expedition to New Guinea. The animal which was collected from the Utakwa River, Irian Jaya was given to Thomas only weeks (or at the most months) after *P. murex* had appeared in print. This specimen was not only larger than the *P. murex* type but it represented (and still represents) one of the largest female *Murexia longicaudata* ever recorded. Thomas' description of *P. murex* was based on differences in size between it and the Leiden *P. longicaudata*

holotype. For four diagnostic measurements, the actual differences in size are of the following magnitude (in millimetres, see paragraphs 2 and 4 earlier) $M^{1-4} = 0.58$, $M_{1-4} = 0.63$, M^2 width = 0.21, M_2 width = 0.02. The difference between the new Utakwa River specimen and the Leiden holotype was of the following order: $M^{1-4} = 1.87$, $M_{1-4} = 1.87$, M^2 width = 0.41, M_2 width = 0.44; and between the Utakwa River specimen and *P. murex*: $M^{1-4} = 1.29$, $M_{1-4} = 1.24$, M^2 width = 0.20, M_2 width = 0.45. Using Thomas' criterion of size, if any specimen other than *longicaudata* rated full specific status then it was the Utakwa River specimen. Thomas, now in apparent anticipation of the enormous size variation within the species, chose to describe it as *aspera*, a subspecies of *P. murex*. (He was apparently unaware of 2 gigantic specimens of *Murexia* in Berlin (ZM13693, ZM60535) collected from the Urwald des Oertzengebirges, Irian Jaya in 1908 and from Astrolabe Bay, PNG in 1888).

Although Thomas noted in the *P. murex aspera* (f) holotype the longer molar row, broader muzzle and shorter premolar row compared to the *P. murex* (m) holotype, his few specimens could not reveal to him that these features were

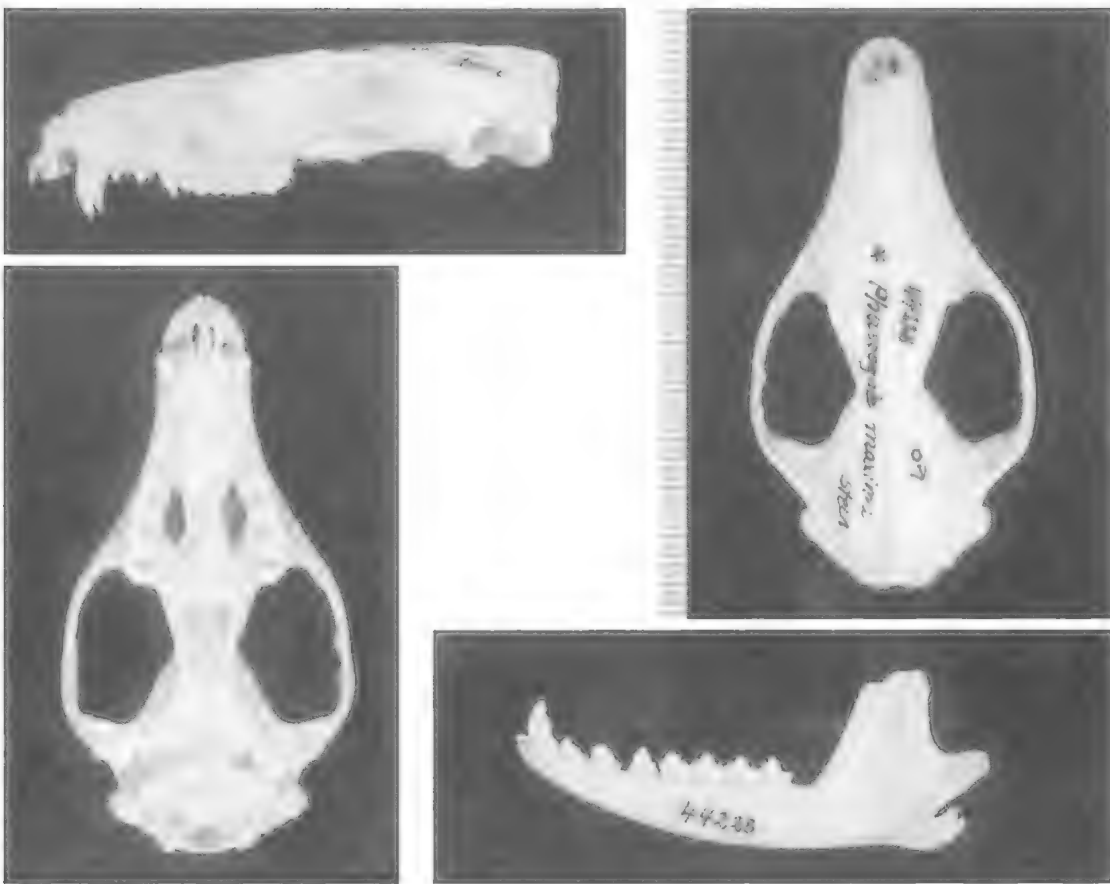


FIG. 28. Holotype of *Phascogale maxima* Stein, 1932. ZM 44228, cranium and dentary. Sex =m; BL = 53.69; ZW = 30.41; IO = 7.08; QBW = 17.24; IBW = 10.44; R-LC¹ = 9.58; R-LM¹ = 16.54; R-LM² = 19.99; R-LM³ = 23.93; R-LM⁴ = 13.80; M²W = 3.21; I¹-M⁴ = 29.41; P¹⁻³ = 8.67; M¹⁻⁴ = 11.54; Dent = 44.12; I¹-M⁴ = 44.89; P¹⁻³ = 9.20; M¹⁻⁴ = 12.42; M²W = 1.86.

normal examples of sexual dimorphism seen across the range of *Murexia*.

It is not clear if Stein (1932) was aware of *P. murex* and *P. murex aspera* when he described *P. maxima*, but no mention is made of them in his diagnosis. There is little doubt though, that even with this knowledge, Stein would have proceeded and named *maxima* on the basis of its enormous proportions. Specimens available to him at Berlin (probably) comprised ZM13693 and ZM60535, the two very large males mentioned earlier, (both larger than Stein's type) and one small specimen (ZM45801) which was of similar proportions to the Leiden *P. longicaudata*. (To my knowledge ZM13693 in East Berlin still represents the largest specimen ever recorded).

In his description Stein noted one very significant feature which up until then had gone unemphasised in *Murexia* — that of the upward gradient in lower premolar size from P₁ to P₃, a feature rarely encountered in the Dasyuridae, '... untere Pramolaren von einander und durch geringeren Zunschenraum auch von den Molaren getrennt, an Grosse zunehmend, so dab der letzte Pramolar die Hohe der Molaren hat'. (Stein 1932: 254-5).

Five years later in an extraordinary, uncharacteristically brief footnote, Tate & Archbold (1937) announced the new subgenus *Murexia* (for reasons which were diagnostically obscure and overlapping into other genera). The type they assigned to *Murexia* was *Phascogale murex* Thomas and to it they referred *P. m. aspera* Thomas and *P. maxima* Stein. At this stage Tate &

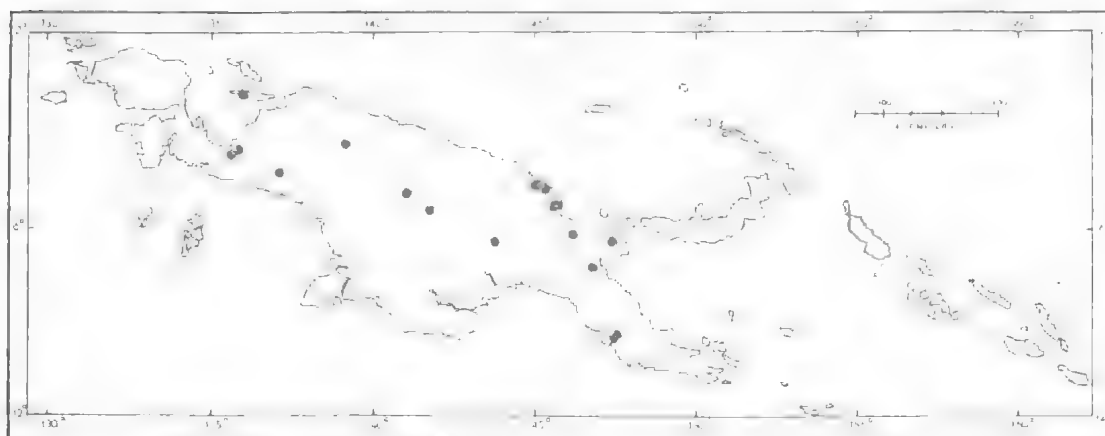


FIG. 29. Distribution of *Murexia longicaudata*.

Archbold could not assign *longicaudata* to a sub-generic position, but considered it most closely related to *Phascogale tafa* (= *Phascomurexia naso*). They also made no mention of Stein's observation of the lower premolar gradient until 10 years later when Tate (1947) noted this feature in *Murexia* and combined it with the characteristic incisor gradient and P4 morphology to suggest that *Murexia* was 'possibly the little-altered descendent of the early Tertiary marsupial that evolved into *Thylacinus*' (p. 117), a suggestion which has received considerable attention from Archer (1976b, 1982a, b). Tate (1947) acknowledged synonymy of *P. murex* Thomas and *P. longicaudata* Schlegel and recognised 3 subspecies; *longicaudata*, *murex* and *aspera* (wherein *maxima* was given junior synonymy). 'The only difference of importance between *longicaudata*, *murex*, *aspera* and *maxima*, after age and sex characters have been discounted is the one of size' (p.116).

Hereafter Tate's case for these 3 subspecies becomes very suspect. While *longicaudata* from Aru Islands was very small and the *maxima* race (within *longicaudata aspera*) was extremely large, the diagnosis of the intermediate subspecies *longicaudata murex* (Huon Peninsula) does not stand up to scrutiny. If, as Tate (1947:116, 118) suggested the race *aspera*, which was based on '... a young female ...' (in fact a lactating adult), was also represented by those specimens collected in the Gebroeders by F. Shaw Mayer ('... the morphological range of the smaller-sized group readily includes not only Thomas' type of *aspera* but also a series collected

by Shaw Mayer ...') then on the breadth of the range it is bold to suggest that there are significant grounds upon which to recognise *murex* as a valid (smaller) subspecies; e.g., measurements (in mm) for the *murex* type adult ♂ from Sattelburg, Irian Jaya vs a Gebroeder adult ♂ BMNH 33.6.1.84: ZW = 23.84 vs 22.71, R-LC¹ = 8.12 vs 7.64, R-LM¹ = 15.26 vs 13.63, R-LM² = 17.94 vs 17.03, R-LM³ = 21.01 vs 19.68, I¹-M¹ = 24.12 vs 23.32, M¹⁻⁴ = 9.08 vs 10.18, P¹⁻³ = 7.85 vs 6.66, M² width = 2.58 vs 2.74, Dent length = 36.08 vs 33.27, I₁-M₂ = 21.47 vs 20.86, M₁₋₄ = 10.03 vs 10.66, P₁₋₃ = 8.23 vs 7.04, M₂ width = 1.54 vs 1.66.

While Tate (1947) asserted that the type of *murex* was '... still unique ...' and '... smaller than any other mainland race ...' (p. 116) he ignored the rest of the Shaw Mayer collection made 2 years later (1932) in the Kratke Mts (at 1200m) and which consisted of adult males (e.g. BMNH 50.1400, 50.1401, 50.1404, 50.1406) all of which were much smaller than the *murex* type and scarcely larger than the *longicaudata* type.

Laurie & Hill (1954) however, did take note of the Mt Kratke specimens and referred to *murex* as a junior synonym of the small *longicaudata longicaudata*. The two other subspecies they recognised were *longicaudata aspera* (which includes *maxima*) and *longicaudata parva* (here regarded as *Phascomurexia naso*). *Murexia rothschildi* they regarded as the second *Murexia* species.

As far as I am aware there have been no subsequent references to subspecific forms of *Murexia* (apart from those referring to the dubious nature of *longicaudata parva*) since Laurie &

TABLE 4. Absolute measurements for *Murexia longicaudata*. See 'Methods' for limits of measured dimensions and Table 1 (caption) for abbreviations.

Measurement		N	mean±r	OR	SD	V	CV
BL	Male	28	46.45±1.51	33.26-59.03	8.00	64.06	17.22
	Female	12	37.55±1.10	31.28-44.47	3.81	14.48	10.15
	Total	41	43.64±1.26	31.28-59.03	8.06	65.02	18.47
ZW	M	28	26.86±0.75	19.55-34.45	3.98	15.86	14.82
	F	12	22.20±0.62	18.64-25.67	2.16	4.68	9.73
	T	42	25.33±0.63	18.64-34.45	4.08	16.68	16.11
IOW	M	29	7.69±0.09	7.01-8.69	0.46	0.22	5.98
	F	12	8.06±0.11	7.29-8.69	0.39	0.15	4.84
	T	43	7.81±0.07	7.01-8.69	0.47	0.22	6.02
OBW	M	28	15.06±0.33	11.80-17.95	1.72	2.95	11.42
	F	12	13.63±0.34	12.03-15.41	1.18	1.40	8.66
	T	42	14.59±0.26	11.80-17.95	1.69	2.84	11.58
IBW	M	29	8.85±0.29	6.33-11.78	1.59	2.54	17.97
	F	12	7.56±0.27	5.81-9.06	0.95	0.91	12.57
	T	43	8.44±0.23	5.81-11.78	1.53	2.34	18.13
R-LC ¹	M	28	8.89±0.27	6.50-11.31	1.44	2.07	16.20
	F	12	7.35±0.26	5.94-8.93	0.89	0.79	12.11
	T	42	8.40±0.22	5.94-11.31	1.45	2.11	17.26
R-LM ¹	M	28	15.31±0.36	11.96-18.40	1.92	3.67	12.54
	F	12	13.47±0.41	11.45-16.49	1.42	2.01	10.54
	T	42	14.71±0.30	11.45-18.40	1.94	3.77	13.19
R-LM ²	M	27	18.55±0.41	14.63-21.77	2.14	4.58	11.54
	F	12	16.28±0.48	13.84-19.13	1.65	2.71	10.14
	T	41	17.80±0.35	13.84-21.77	2.22	4.92	12.47
R-LM ³	M	28	22.16±0.50	17.54-26.18	2.66	7.06	12.00
	F	12	19.30±0.58	16.26-22.73	2.01	4.05	10.41
	T	42	21.24±0.43	16.26-26.18	2.76	7.64	12.99
R-LM ¹ T	M	28	12.45±0.29	9.67-14.71	1.54	2.38	12.37
	F	12	10.95±0.33	9.23-12.75	1.14	1.30	10.41
	T	42	11.95±0.24	9.23-14.71	1.58	2.50	13.22
I ¹ -M ⁴	M	29	26.22±0.71	20.32-32.57	3.80	14.44	14.49
	F	11	22.14±0.60	18.48-25.99	1.99	3.97	7.59
	T	42	25.01±0.59	18.48-32.57	3.80	14.42	15.19
P ¹⁻³	M	19	8.11±0.30	5.28-10.91	1.63	2.66	20.10
	F	12	6.09±0.22	4.77-7.54	0.77	0.60	12.64
	T	43	7.49±0.25	4.77-10.91	1.67	2.78	22.30
M ¹⁻⁴	M	29	10.31±0.20	8.76-12.59	1.06	1.11	10.28
	F	12	9.59±0.21	8.69-10.77	0.72	0.51	7.51
	T	43	10.10±0.15	8.62-12.59	1.01	1.02	10.00
M ² W	M	29	2.82±0.06	2.25-3.37	0.34	0.12	12.06
	F	12	2.61±0.07	2.29-3.01	0.23	0.05	8.81
	T	43	2.75±0.05	2.25-3.37	0.33	0.11	12.00
Dent	M	29	38.51±1.27	26.62-50.41	6.84	46.74	17.76
	F	12	30.99±0.88	25.92-36.95	3.06	9.33	9.87
	T	43	36.17±1.03	25.92-50.41	6.78	45.97	18.74
I ₁ -M ₄	M	29	24.16±0.98	17.65-44.89	5.26	27.67	21.77
	F	12	19.61±0.49	17.12-22.72	1.69	2.87	8.62
	T	43	22.73±0.74	17.12-44.89	4.88	23.84	21.47
P ₁₋₃	M	29	8.55±0.35	5.36-12.09	1.89	3.56	22.11
	F	12	6.58±0.34	5.12-9.57	1.17	1.36	17.78
	T	43	7.92±0.29	5.12-12.09	1.90	3.61	23.99
M ₁₋₄	M	29	11.17±0.22	9.24-13.17	1.18	1.40	10.56
	F	12	10.30±0.24	8.62-11.55	0.84	0.71	8.16
	T	43	10.90±0.18	8.62-13.17	1.16	1.35	10.64
M ₂ W	M	29	1.74±0.04	1.40-2.21	0.22	0.05	12.64
	F	12	1.64±0.02	1.41-1.90	0.16	0.02	9.76
	T	43	1.71±0.03	1.40-2.21	0.21	0.04	12.28
TL	M	14	439±18.45	326-550	69	4881	15.72
	F	9	345±15.33	290-413	46	2191	13.33
	T	24	398±15.71	290-550	77	6042	19.35
T	M	23	207±7.29	155-283	35	1081	16.91
	F	11	177±5.72	150-215	19	392	10.73
	T	34	197±5.83	150-283	34	1178	17.26
HF	M	21	36.90±1.31	26.5-47	6.00	35.97	16.26
	F	11	32.00±0.88	27-37	2.92	8.55	9.13
	T	32	35.22±1.00	26.5-47	5.65	31.97	16.04
E	M	14	20.86±0.31	19-24	1.17	1.37	5.61
	F	5	20.00±0.49	18-21	1.10	1.20	5.50
	T	20	20.50±0.29	18-24	1.31	1.72	6.39

Hill, 1954). Woolley (1994) accorded full specific recognition, however, to *Murexia aspersa* (sic).

A most interesting feature in the history of *longicaudata* taxonomy is the absence of comment regarding the gross malformation in the holotype skull. The specimen was originally displayed as a mount (? hence the missing basicranium and lack of cranial and dental measurements accompanying the type description). But it must have been extracted prior to 1880 for Thomas lists its critical measurements in his Catalogue (1888: 299). Tate (1947) referred to the additional lower incisor as '... an anomalous (fourth) incisive tooth, possibly a milk tooth (?)' (p. 117), but the severely undershot dentary, crushed and broad premolars, incompletely erupted C^1 , inwardly folded upper incisors and the abnormal height of the dentary below the premolars have always gone unstated.

DISTRIBUTION. *M. longicaudata* is widely distributed throughout Irian Jaya and PNG in lower to mid-montane forests below 1800m (Fig. 29). Floristic details of collection localities appear in Archbold et al., (1942: 231-243).

REPRODUCTION. All pouches examined contained 4 teats. Lactating females had been collected in (dates included in parentheses) February (13, 17), March (22), April (2, 25), June (17, 27), August (10), December (1).

DESCRIPTION. *Mean Measurements* (mm). External: total length (head, body, tail) TL (δ) 439 (η) 345; hind foot (su) HF (δ) 36.90 (η) 32.00; ear (notch) E (δ) 20.86 (η) 20.00. Skull: basicranial length BL (δ) 46.45 (η) 37.55; M^{1-4} length (δ) 10.31 (η) 9.59; M^2 width (δ) 2.82 (η) 2.61. (Table 4).

Postmetatarsal and Calcaneal Pads. Of all males (adult, juvenile and subadult) examined for postmetatarsal and calcaneal pads (N = 18), 44% (N = 8) exhibited a single postmetatarsal pad on both left and right hind foot. Three males (17%) exhibited a single postmetatarsal pad and a single calcaneal pad on both left and right hind foot.

Of all females examined for postmetatarsal and calcaneal pads (N = 4), 50% (N = 2) exhibited a single postmetatarsal pad on both left and right hind foot. No females exhibited calcaneal pads.

P4 Morphology. Only 3 juveniles were available for the study of deciduous premolars (AMNH 101970, AMNH 152035 and BMNH 33.6.1.71). In all cases L and RP^4 were 3-rooted with the paracone and metacone coalescing into one

major cusp. The protocone was well developed, as was styler cup B and the metastylid. In the lower molars L and RP^4 were single-rooted, formless spurs.

Body Size. Adult male *M. longicaudata* are significantly larger than adult females. (For basicranial length BL in males mean = 46.54mm, N = 28; for females mean = 37.55mm, N = 12, $P < 0.001$). Females never attained the massive size seen in males, and the largest measure of BL recorded for an adult female (44.47mm) was less than the mean BL for males. Some of the largest specimens examined (ZM 60532, BL = 57.33 and ZM 13693, BL = 59.03) displayed dental abnormalities. In ZM 60532 an extra cusp is present on the posterior edge of the M^1 protocone. In ZM 13693 two small caniniform teeth incline against the posterobuccal surface of the LC^1 .

The largest of adult male specimens examined (i.e., mean BL = 50mm, N = 9) were from localities north of 6°00'S (i.e., 01°45'S - 5°28'S). Within this latitudinal range, body size varied significantly and inversely with altitude (e.g., at altitudes above 900m a.s.l. mean BL for adult males = 45.97mm; at or below 900m mean BL = 54.24mm ($P < 0.01$). South of 6°00'S a similar inverse relationship existed between body size and altitude (e.g., at altitudes above 900m a.s.l. mean BL for adult males = 34.43mm; at or below 900m mean BL = 46.56mm ($P < 0.001$).

The largest adult female specimens examined (i.e., mean BL = 40mm, N = 3) were also from northern localities (i.e., 3°30'S, at Bernhard Camp, 75m - 850m a.s.l.). North of 6°00'S body size varied significantly and inversely with altitude (e.g. at altitudes above 900m a.s.l. mean BL for adult females = 37.73mm; at or below 900m mean BL = 41.40mm ($P < 0.05$). South of 6°00'S there was no significant relationship between body size and altitude in females.

The smallest adult males examined (i.e., mean BL = 38mm, N = 7) were from localities in 4°48'S 145°20'E - 6°32'S 147°17'E (i.e., Kratake Mts, Atitau, Gang Creek, at 1220m - 1311m a.s.l.).

The smallest adult females examined (i.e., mean BL = 35mm, N = 3) were from localities in 3°39'S 135°56'E - 6°32'S 147°17'E (i.e., The Gebroeders, Gang Ck, at 1375m - 1525m a.s.l.).

Premolar Diastemata. In the upper premolar row of adult males, largest diastemata occurred most frequently between P^2 - P^3 (41%, N = 9) and P^3 - M^1 (41%, N = 9), while 18% (N = 4) exhibited no diast- emata in the upper premolar row. No

specimen had the largest upper premolar diastema between P^1 - P^2 .

In the lower premolar row of adult males, largest diastemata occurred most frequently between P_3 - M_1 (55%, $N=12$), less frequently between P_2 - P_3 (36%, $N=8$), while 9% ($N=2$) exhibited no diastema in the lower premolar row. No specimen exhibited a condition where the largest lower premolar diastema occurred between P_1 - P_2 .

In the upper premolar row of adult females, largest diastemata occurred most frequently between P^2 - P^3 (89%, $N=8$), while 11% ($N=1$) exhibited no diastema in the upper premolar row. No specimens exhibited a condition where the largest upper premolar diastema occurred either between P^1 - P^2 or between P^3 - M^1 .

In the lower premolar row of adult females, largest diastemata occurred most frequently between P_2 - P_3 (44%, $N=4$), less frequently between P_3 - M_1 (11%, $N=1$), while 44% ($N=1$) exhibited no diastema in the lower premolar row. No specimen exhibited a condition where the largest lower premolar diastema occurred between P_1 - P_2 .

SPECIMENS EXAMINED. Astrolabe Ra., 450m, 9°30'S 147°20'E (AMNH 108558); Astrolabe Ra., 520m, 9°30'S 147°20'E (AMNH 108556-108557); Atitau, 1158m, 4°48'S 145°20'E (AMNH 198720); Bernhard Camp, 75m, 3°30'S 139°12'E (AMNH 152014-152018, AMNH 152035); Bernhard Camp 4km SW, 850m, 3°30'S 139°12'E (AMNH 151997-2000); Derimapa Mt., 1220-1525m, 3°50'S 135°43'E (BMNH 1939.3235); Derimapa Mt., 1524m, 3°50'S 135°43'E (AMNH 101970-101971, BMNH 33.6.1.71-72, BMNH 336170); Derimapa Mt., 1830m, 3°50'S 135°43'S (BMNH 1939.3236); Derimapa Mt., 3°50'S 135°43'E (BMNH 33.6.1.84); Gang Creek, 1311m, 6°32'S 147°17'E (AMNH 194712); Gang Creek, 1372m, 3°62'S 147°17'E (AMNH 194710-11); Yapen I., 50m, 1°45'S 136°10'E (ZM 44228); Josephstaal, 4°44'S 145°00'E (AMNH 198721); Kratke Mts, 1200-1525m, 6°19'S 146°05'E (BMNH 50.1404-05); Kratke Mts, 1200m, 6°19'S 146°05'E (BMNH 50.1400, BMNH 50.1402); Kratke Mts, 1311m, 6°19'S 146°05'E (BMNH 50.1406); Kratke Mts, 6°19'S 146°05'E (BMNH 50.1401); Mabion Mt., 750m, 5°32'S 141°44'E (AMNH 105022); Namosado, 6°15'S 142°47'E (AMNH 14858, M15611); Oertzen Mts, 5m, 5°28'S 145°32'E (ZM 13693); Ogerannangim Sarvaged, 1785m, 3°39'S 135°56'E (ZM 45801); Sattelburg, 290m, 6°30'S 147°43'E (BMNH 12.2.4.1); Sibil Valley, 1250m, 5°00'S 141°00'E (RMNH 224, RMNH 16946); Sogeri, 450m, 9°25'S 147°26'E (AMNH 108554-5); Stephansort, 5m, 5°27'S 145°45'E (ZM 60532); The Gebroeders, 1525m, 3°39'S 135°56'E (AMNH 101972-3); Utakwa R., 762m, 4°24'S 137°12'E (BMNH 13.6.18.90); Wanuma, 671m, 4°51'S 145°19'E (AMNH 198719); Wau, 1159m, 7°20'S

146°43'E (AMNH 221630); Wonoembai Aru Is, 100m, 6°00'S 134°30'E (RMNH 35153, BMNH 50.1403).

Paramurexia gen. nov.

Phascogale (in part) Temminck, 1824.

Murexia (subgenus) (in part) Tate & Archbold, 1937.

TYPE AND ONLY SPECIES. *Phascogale* (*Murexia*) *rothschildi* Tate, 1938: 58.

GENERIC DIAGNOSIS. Broad, black, dorsal body stripe which commences at the nose and terminates at the base of the tail. M^1 very broad, with wide protocone and complete anterior cingulum, the anterior margin of this tooth is straight or anteriorly convex, but never indented or concave. Tail longer than head-body length.

It is distinguished from *Phascolosorex* by the narrow width of its body stripe and by its lack of reduced premolars, from *Myoictis* by its single dorsal body stripe and by its lack of reduced premolars, and from *Neophascogale* by its lack of reduced premolars and lack of a thickly-haired, white-tipped tail.

Paramurexia is separable from *Micromurexia*, *Paramurexia*, *Murexechinus* and *Murexia* by its single black, longitudinal head-body stripe and black facial mask.

Paramurexia rothschildi (Tate, 1938) (Figs 30, 31)

Phascogale (*Murexia*) *rothschildi* Tate, 1938: 58.

HOLOTYPE. BMNH 1939.3233. Adult ♂ study skin and skull extracted (skin in good condition though slightly faded, skull in good condition).

TYPE LOCALITY. Head of the Aroa River, PNG, 8°50'S 147°06'E. Probably at 'about ± 4000 feet' (Tate, 1947). Coll. A.S. Meek, May 28, 1905.

DIAGNOSIS. As for genus.

DESCRIPTION. HOLOTYPE. *Pelage* (Fig. 30). Fur of mid-back dorsal stripe 6mm long with basal half Slate Gray and apical half Fuscous Black. Similarly pigmented guard hairs 7.4mm long are interspersed through the dorsal stripe. Fur of the mid-back immediately outside the 'black' dorsal stripe is 6mm long with basal 3.7mm Slate Colour, median 1.5mm Clay Colour and apical 0.8mm Fuscous Black. Fur beside the stripe thus appears overall to be a Saccardo's Umber. Guard hairs are interspersed through this fur and are 7.5mm long on the rump and reduce to 3mm on the crown of the head. Fur on and below the shoulders, thighs, flanks and chin lacks the black tips or coarse guard hairs and these areas and the belly appear as Cinnamon Buff.

The black dorsal stripe is 15mm at its widest. A distinct head-stripe runs from the tip of the nose expanding in width to the mid-back. Another less distinct stripe originates among the mystacial vibrissae on each side. These Fuscous Black hairs progress posteriorly, passing over and under the eye and degenerate just to the anterior of the pinnae. A distinct eye-ring results from the combined effect of these dark hairs and the skin of the eyelids, which is darkly pigmented. A narrow band of short, black eyelash hairs completely encircles each eye. The remainder of the fur under each eye is a light fawn (Tawny Olive). The soft, ventral fur is 7mm long on the belly. The basal 4mm is Mouse Gray and the apical 3mm is Cinnamon Buff. The belly appears overall as Chamois coloured. Forefeet and hindfeet are thinly covered with Buffy Brown hairs. The tail is weakly bicoloured with mid-dorsal hairs 1.6mm long (Fuscous Black) and dorsal tip hairs 2mm long (Fuscous Black). Mid-ventral hairs are 4mm long and increase to 8mm at the tip. The full ventral crest begins as Fuscous-coloured but becomes silvery toward the tip.

Vibrissae. Approximately 26 mystacial vibrissae occur on each side and are up to 30mm long. The more dorsal vibrissae are Fuscous Black, while those lower are colourless; supra-orbital vibrissae (Fuscous Black) number 2 (left) and 2 (right); genals (Fuscous Black and colourless) number 10 (left) and 10 (right); ulna-carpals (colourless) number 6 each side; submentals (colourless) number 2.

Tail. The tail is longer than head and body. It is thin and tapers toward the tip.

Hindfoot (Fig. 33). The interdigital pads are separate. The apical granule is enlarged, elongate and striate. A greatly enlarged auxillary granule occurs outside the third interdigital pad. Hallucal and post-hallucal pads are fused and very elongate and broad. The metatarsal pad is greatly enlarged and elongate almost contacting the third interdigital pad. A very large, elongate calcaneal pad wraps around the heel. All pads are striate.

Ears. It was not possible to determine the state of the pinnae and supratragus from the type specimen. In other specimens, however, the supratragus is folded.

Dentition (Fig. 31). Upper Incisors: Left and (particularly) right I^1 are badly worn. They appear to have been narrow, peg-like and procumbent, taller crowned than all other incisors and separated from I^2 by a diastema. (In

other specimens e.g., BMNH 50.1107, there is a small, auxillary posterior cusp on I^1 which gives I^1 the appearance of the tip of a crochet-hook). In crown size $I^4 > I^3 > I^2$. All upper incisors lack buccal cingula yet the crowns and roots are easily identified. I^4 carries no anterior or posterior cusps. The roots of I^4 are narrow.

Upper Canines: C^1 is thick, short and blunt with an indistinct boundary between root and crown. There is no buccal or lingual cingulum, and there is no anterior or posterior cusp.

Upper Premolars: The premolar row is short and the premolars broad with P^1 and P^2 bearing heavy posterolingual lobes. The premolars are, however, not crushed against one another. Slight diastemata occur between C^1 and P^1 , P^1 and P^2 and P^2 and P^3 . In crown height $P^3 > P^2 > P^1$. Small anterior and posterior cusps occur on P^1 and P^2 . A small posterior cusp is present on P^3 .

Upper Molars: Molars are heavily worn. The posterior tip of P^3 lies in the parastylar corner of M^1 but lingual to, and well below stylar cusp A. The anterior cingulum below stylar cusp B is short, broad and just complete. Stylar cusp B and the paracone are relatively worn and a minute protoconule is present at the base of the paracone apex. The minute protoconule is accompanied by a small bulge of enamel directly below it on the face of the anterior protocrista. The paracone on M^1 is very narrow and pinched. Stylar cusp C is not visible on either LM^1 or RM^1 and stylar cusp E is not visible. M^1 has a weak posterior cingulum.

In M^2 the broad anterior cingulum which contacts the metastylar corner of M^1 tapers quickly as it progresses down and along the base of the paracrista and finally degenerates labially to, and well before the trigon basin. No protoconule is visible. M^2 lacks stylar cusps A, C and E. Stylar cusp D is slightly reduced, narrow and there is a weak posterior cingulum.

In M^3 the anterior cingulum is as short as that of M^2 , it becomes indistinct after covering 1/3 the distance between stylar cusp B and the base of the paracone. There is slight evidence of an anterior cingulum at the base of the paracone and there is no protoconule or protocone enamel bulge. Stylar cusp D is reduced to a very long, sharp crest. Stylar cusp E is absent, as is stylar cusp C.

In M^4 the metastylar corner is poorly developed. The broad anterior cingulum terminates quickly away from the metastylar corner of M^3 and a posterior cingulum is absent. The protocone is much reduced and narrow. In

occlusal view the angle made between the post-protocrista and the post-paracrista is close to 135° , reflecting little metacone development.

Lower Incisors: The small first lower incisor is larger in crown height than I_2 . I_1 and I_2 are oval in anterolateral view and gouge-like in occlusal view. I_2 is larger in crown height than I_3 . I_3 is incisiform in lateral view with a very weak posterior cusp at the base of the crest which descends posteriorly from the apex of the primary cusp. The lower canine rests against this posterior cusp. In occlusal view, a small notch separates the posterior cusp from the weak posterolingual lobe, and crown enamel of the primary and posterior cusps scarcely folds lingually such that the crest of the two cusps barely impacts on the tooth lingually.

Lower Canines: C_1 is caniniform, with forward, upward projection and strong curvature from root to crown tip. It has weak buccal and lingual cingulation and no posterior cusp. Some thegotic wear is present on the posterior surface of C_1 .

Lower Premolars: Although the premolar row is short and the premolars broad, there are small diastemata between all premolars and between C_1 and P_1 and P_3 and M_1 . All premolars are very strongly cingulated buccally and lingually. $P_2 \approx P_3 > P_1$. P_1 is very broad and strongly built with heavy labial, lingual and posterior cingula as well as an anterior cusp. The bulk of each premolar is concentrated posteriorly to a line drawn transversely through the middle of the 2 premolar roots. P_1 (only) shows heavy posterolingual lobes.

Lower Molars: All molars are broad. The M_1 talonid is wider than the trigonid and the anterior cingulum is absent. The paraconid is greatly reduced to a minute bump of enamel.

The metacristid is roughly oblique to the long axis of the dentary while the hypocristid is very oblique. The cristid obliqua is very short and extends from the hypoconid to the posterior wall of the trigonid intersecting the trigonid at a point slightly lingual to that point directly below the tip of the protoconid. The hypocristid terminates midway between the hypoconid and the metastylid. There is no entoconid. From the base of the metaconid posteriorly, the talonid endoloph follows the line of the dentary until the base of the hypoconulid. The metaconid is badly worn.

In M_2 the trigonid is slightly narrower than the talonid. The anterior cingulum is poorly developed, terminating lingually in a weak

parastylid notch into which the hypoconulid of M_1 is tucked. The buccal cingulum is strong. A narrow, very weak, posterior cingulum extends from the hypoconulid to the posterior base of the hypoconid. The paraconid is worn and is the smallest trigonid cusp. There is no entoconid. The cristid obliqua extends from the hypoconulid to the posterior wall of the trigonid intersecting the trigonid at a point directly below the tip of the protoconid but well buccal to the metacristid fissure. The hypocristid extends from half way along the worn hypoconulid to the tip of hypoconid. From the base of the metaconid posteriorly, the endoloph follows the line of the dentary axis.

In M_3 the trigonid is slightly narrower than the talonid. A weak parastylid wraps around the hypoconulid of M_2 and there is a very weak anterior cingulum on M_4 . Buccal and posterior cingula are as in M_2 but more poorly developed. A reduced cristid obliqua intersects the trigonid at a point well lingual to the longitudinal vertical midline drawn through the tip of the protoconid, but just buccal to the metacristid fissure. There is no entoconid on M_3 . The endoloph on the talonid of M_4 takes a more buccal orientation than that seen in M_2 . The rest of M_3 morphology is as in M_2 except that a small crest runs down from the hypoconulid to the beginning of the hypocristid.

In M_4 the trigonid is wider than the talonid. There is no anterior cingulum. A posterior cingulum is absent. Of the three main trigonid cusps the metaconid is equal in height to the paraconid but both are dwarfed by the protoconid. The hypoconid of the M_4 talonid is similar in size to M_3 . Between the hypoconid and the base of the metacristid, the cristid obliqua forms low, weak crest which degenerates before contacting the trigonid wall. A significant feature of the M_4 morphology is the reduction of talonid crown enamel below the cristid obliqua which results in the talonid appearing (in occlusal view) as a narrow oblique spur jutting off the trigonid wall. There is no entoconid and no cusps represent the hypoconulid or hypoconid. Small worn shelves, however, represent these cusps.

Skull (Fig. 31). The holotype exhibits minor fluting of the nasals. Alisphenoid tympanic bullae are widely separated and minutely inflated. The foramen pseudovalle is large and not bisected by the bridge of the alisphenoid. The eustachean canal opening is large. The premaxillary vacuity (3.87mm long) extends from the level of the I^1 root back to the level of the posterior edge of the C^1 root. The very small

maxillary vacuity (6.62mm long) extends from the level of the posterior root of P^3 back to the level of the metacone root of M^3 . There are no palatine vacuities present.

ADDITIONAL DIAGNOSTIC FEATURES

Paramurexia differs from all other dasyurids in the combination of the following features: 1, I^1 lightly built, curved (more claw-like) and slightly laterally compressed with heavier crown than *Micromurexia*, *Murexia* or *Phascomurexia*; 2, I^1 and I^2 widely separated; 3, a slightly cingulated upper incisor row where $I^2 < I^3 < I^1$; 4, I^4 without a posterior cusp; 5, upper canines long, thin (but bulkier and shorter than in *Micromurexia*, *Paramurexia*, and *Murexia*). The root and crown are more differentiated than in those genera and there is no posterior cusp; 6, an upper premolar row in which the moderately cingulated teeth are uncrowded from C^1 to P^2 , but where P^3 usually touches P^2 and M^1 ; 7, P^1 and P^2 are rounded and show postero-lingual lobing; 8, M^1 very broad, with wide protocone and complete anterior cingulum, the anterior margin of this tooth is straight or anteriorly convex, but not indented or concave; 9, M^1 and M^2 stylar cusp B large (slightly smaller than stylar cusp D in M^1 , subequal in M^2); 10, M^4 protocone more narrow than in *Micromurexia* but anterior cingulum complete; 11, M^1 and M^2 stylar cusp D a relatively low crest rather than a tall cone; 12, M^4 metacone reduced more than in *Micromurexia*, *Paramurexia* and *Murexia*; 13, a lightly cingulated lower premolar row in which the more rounded teeth are slightly crushed, and where P_3 is smaller than P_2 ; 14, cingulated P_3 ; 15, M_3 talonid width subequal to the trigonid; 16, paraconid on M_1 more reduced than in *Micromurexia*, *Paramurexia* and *Murexia*; 17, three very poorly developed cusps on the M_4 talonid; 18, entoconid of M_2 is more reduced than in *Micromurexia*, *Paramurexia* and *Murexia*; 19, metacristids and hypocristids are not transverse to the long axis of the dentary; 20, skull elongate and domed; 21, fluted nasals; 22, poorly developed tympanic wing of the alisphoid with contrasting expansion of the pars mastoidea and adjacent squamosal; 23, presence of a long postmetatarsal pad and calcaneal pad on hind foot; 24, tail thinly haired with short hairs and weak, light-coloured ventral crest developing at the distal end, the tail being longer than the head-body length; 25, polyoestrous and nipple number low (4); 26, penile morphology is simple.

In addition to those features noted in the generic diagnosis *P. rothschildi* is immediately separable from *Micromurexia habbema* by its larger (the ranges (R) associated with each measurement do not overlap, Table 5); basicranial length BL, zygomatic width ZW, basicranial width measured outside bullae OBW, inside bullae width IBW, rostral widths R-LC¹, R-LM¹, R-LM², R-LM³, maxilla width R-LM¹T, upper tooth row I^1 -M⁴, lower tooth row I_1 -M₄, lower molar row M_{1-4} , and lower second molar width M_2 W. *P. rothschildi* also differs significantly ($P < 0.001$) from *M. habbema* as follows: longer upper premolar row P^{1-3} (4.77: 3.85); longer dentary Dent (28.33: 21.46); longer lower premolar row P_{1-3} (5.03: 4.08); longer tail T (168: 135); longer ear E (19.92: 16.95); longer hind foot HF (27: 22); strongly curved claws rather than slender, semi-straight claws; hindfeet with post-metatarsal pads.

P. rothschildi is immediately separable from *Phascomurexia naso* by its wider second molars. (For M^2 in *P. rothschildi* mean=2.45, R=2.32-2.69; in *P. naso* mean=2.02, R=1.89-2.22. For M_2 in *P. rothschildi* mean=1.56, R=1.46-1.72; in *P. naso* mean=1.31, R=1.23-1.43). *P. rothschildi* also differs significantly ($P < 0.001$) from *naso* as follows: longer basicranial BL (35.41: 30.13); greater zygomatic width ZW (21.29: 17.45); wider basicranium measured outside bullae OBW (13.21: 11.57); wider inside bullae IBW (7.27: 5.81); wider rostrum R-LC¹ (7.72: 5.91), R-LM¹ (12.20: 10.57), R-LM² (14.79: 12.97), R-LM³ (17.65: 15.48); wider maxillae R-LM¹T (10.08: 8.50); longer upper tooth row I^1 -M⁴ (19.68: 17.32); longer upper molar row M^{1-4} (8.71: 7.61); longer dentary Dent (28.33: 24.23); longer lower tooth row I_1 -M₄ (17.39: 15.18); longer lower molar row M_1 -M₄ (9.48: 8.32); post-metatarsal pads on hind feet.

P. rothschildi is immediately separable from *Murexechinus melanurus* by its larger ears. (For E in *rothschildi* mean=19.92, R=19-21.5; in *melanurus* mean=15.83, R=14-18). *P. rothschildi* also differs significantly ($P < 0.001$) from *melanurus* as follows: longer basicranium BL (35.41:26.83); greater zygomatic width ZW (21.29: 16.89); wider outside bullae OBW (13.21:10.99); wider inside bullae IBW (7.27: 5.12); wider rostrum R-LC¹ (7.72:5.43), R-LM¹ (12.20:9.71), R-LM² (14.79:11.91), R-LM³ (17.65:14.12); wider maxillae R-LM¹T (10.08:7.69); longer upper tooth row I^1 -M⁴ (19.68: 14.88); longer upper premolar row P^{1-3} (4.77: 3.37); longer upper molar row M^{1-4} (8.71:

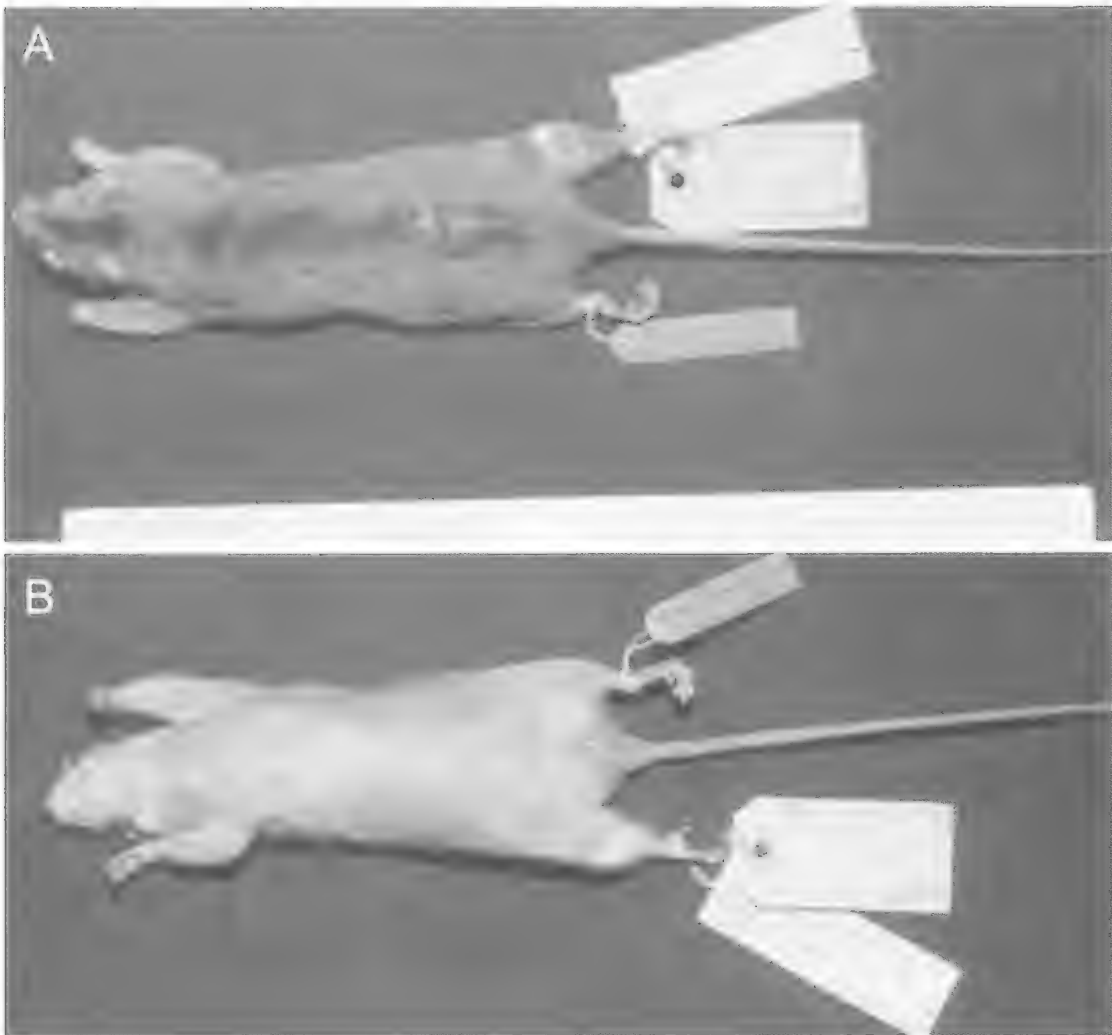


FIG. 30. Holotype of *Paramurexia rothschildi* Tate, 1938. BMNH 1939.3233, study skin; A, dorsal view; B, ventral view. TL = 350mm; HB = 170mm; TV = 180mm; HF = 13mm.

6.78); wider upper second molar M^2W (2.45: 1.89); longer dentary Dent (28.33: 21.31); longer lower tooth row I_1-M_4 (17.39:12.96); longer lower premolar row P_{1-3} (5.03:3.45); longer lower molar row M_{1-4} (9.48:7.37); wider lower second molar M_2W (1.56:1.22); face with black mask rather than rufous post-auricular patches; tail thinly haired with short hairs and weak, light-coloured ventral crest developing at the distal end rather than tail thickly haired a uniform black (sometimes dark brown) with ventral crest hairs long throughout.

P. rothschildi differs significantly ($P < 0.001$) from *Murexia longicaudata* as follows: narrower

skull at $R-LM^2$ (14.79: 17.80) and $R-LM^3$ (17.65: 21.24); shorter upper tooth row I^1-M^4 (19.68: 25.01); shorter upper premolar row P^{1-3} (4.77:7.49); shorter upper molar row M^{1-4} (8.71:10.10); shorter lower premolar row P_{1-3} (4.07:7.92); I^1 broad and claw-like rather than long, narrow and needle-like; premolar row short with premolars crowded and broad rather than premolar row uncrowded with premolars narrow and widely spaced; P^4 single-rooted rather than three-rooted; M^4 without a metacone rather than with a metacone; M_4 without an entoconid; hind foot with large auxillary granule outside the third interdigital pad, elongate metatarsal pad which

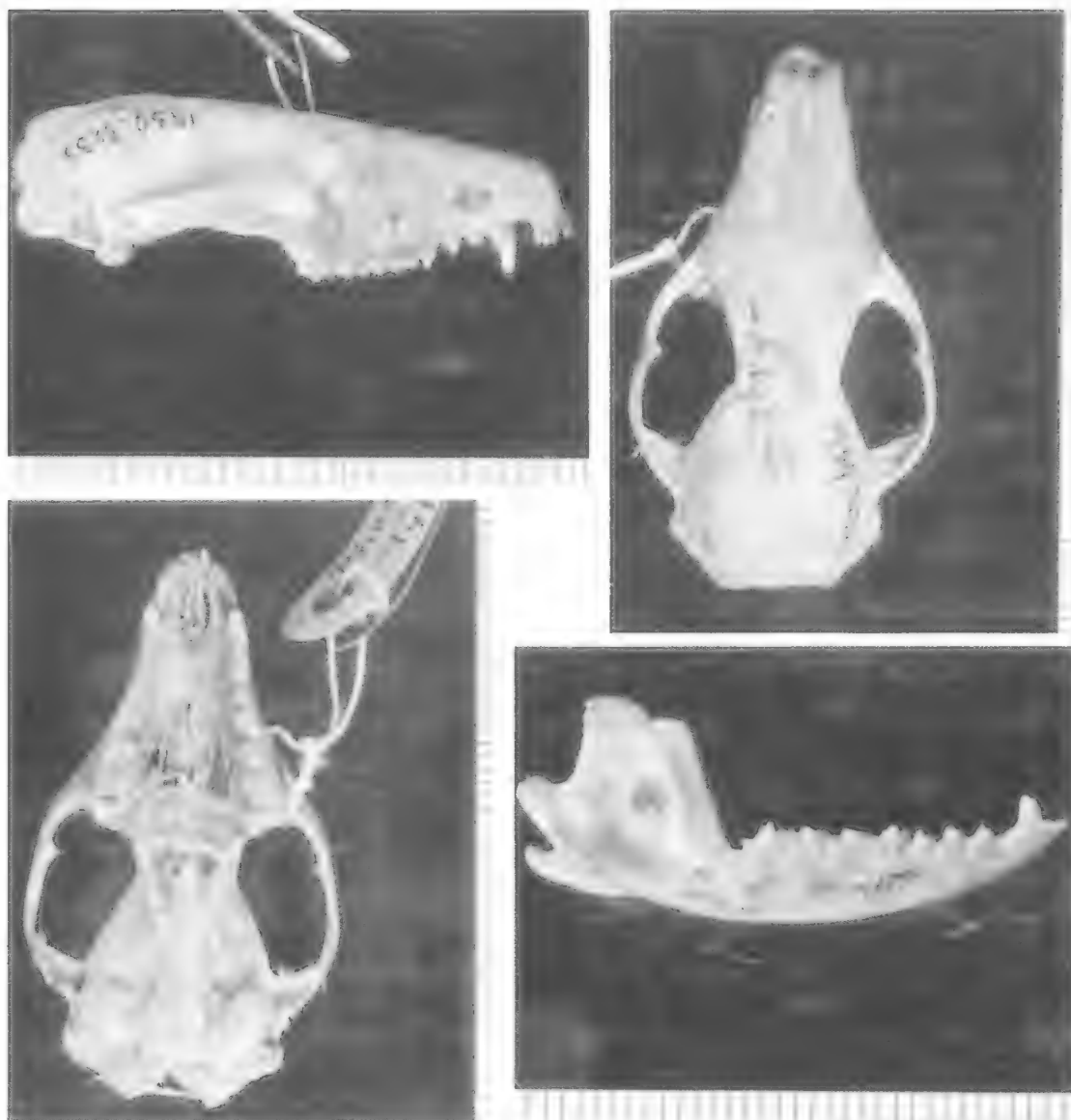


FIG. 31. Holotype of *Paramurexia rothschildi* Tate, 1938. BMNH 1939.3233, cranium and dentary. Sex = m; BL = 40.12; ZW = 24.63; IO = 8.00; OBW = 14.69; IBW = 8.11; R-LC¹ = 7.88; R-LM¹ = 12.72; R-LM² = 14.86; R-LM³ = 19.39; R-LM¹T = 11.32; M²W = 2.69; I¹-M¹ = 21.31; P¹⁻³ = 5.15; M¹⁻⁴ = 9.27; Dent = 32.15; I₁-M₄ = 18.65; P₁₋₃ = 5.30; M₁₋₄ = 9.61; M₂W = 1.72.

almost contacts the third interdigital pad, and highly developed, striate post-metatarsal and calcaneal pads rather than unspecialised.

REMARKS. *Taxonomic History.* Predictably, the history of this beautiful species is uneventful. Since its collection by A.S. Meek in 1905, institutional holdings of *rothschildi* have been bolstered only by the collections of F. Shaw

Mayer (in 1940), W. Hitchcock and R. Schodde (in 1969) and A. Engilis/R.E. Cole (in 1985). Such holdings are even now represented by no more than approximately 16 specimens.

Its distinctive, consistent physical attributes combined with its poor representation in reference collections has conferred on it a stable taxonomic history.

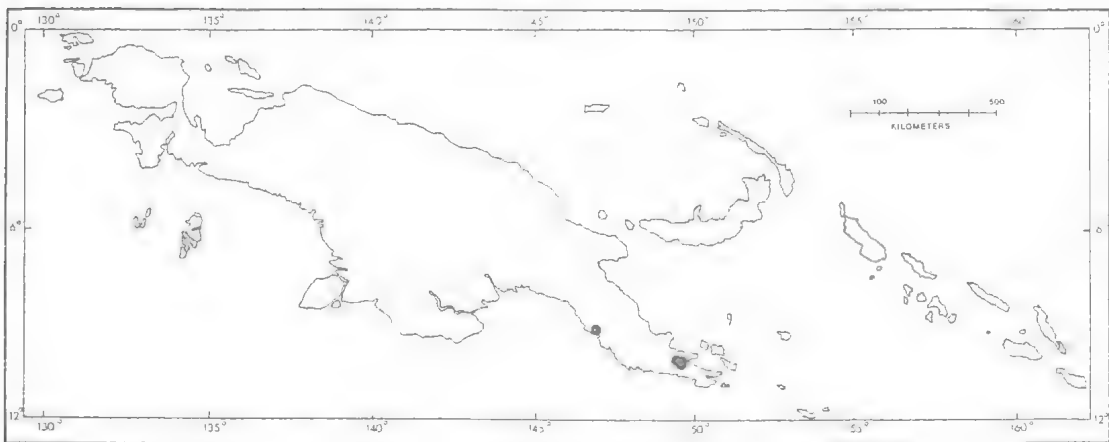


FIG. 32. Distribution of *Paramurexia rothschildi*.

The most interesting feature in the history of *rothschildi* is its anonymity from the time of its collection (1905) until Tate 'came across two specimens' (Tate, 1938) in the Tring Museum in the summer of 1937. Through the Director of the Tring Museum, Karl Jordan, Tate obtained the consent of Lord Rothschild to borrow the material for description. Tate retained the other specimen (paratype) for the American Museum of Natural History and described the species the following year. Rothschild died 27 August 1937, soon after Tate's visit, and before the description was published.

By 1938 Thomas had described species such as *flavipes adusta* (1923), *godmani* (1923), *bella* (1923), *swainsonii mimetes* (1924), *minutissima sinualis* (1926), *mimulus* (1906), *murex* (1913), *murex aspera* (1913), *melanura* (1899), *melanura modesta* (1912), *lorentzi venusta* (1921), *venusta rubrata* (1922), *doriae* (1886) and *daemonellus* (1904), all from the collecting efforts of Sherrin, Tunney, Wilkins, Stalker, Fritsche, the Pratt brothers, Kloss, Loria, and Meek. Some of these inveterate collectors were funded by Rothschild, and it was an established practice from the earliest days of the Tring Museum's *Novitates Zoologicae* until around 1921, for Lord Rothschild to invite Oldfield Thomas from the British Museum to describe the small mammals from such collecting trips. Rothschild's generosity in respect of such opportunities, and the subsequent donation of specimens to the British Museum, was always acknowledged by Thomas (Thomas, 1903a; 1903b; 1904; 1912; 1913; Thomas & Martin, 1920). The reason Thomas missed such an

extraordinary and distinct marsupial as *P. rothschildi* is unknown.

DISTRIBUTION (Fig. 32). From 6, near-coastal localities in the SE tip of PNG, all between 09°56'S - 10°02'S and 147°00'E - 149°43'E.

Heron (1975) suggested that during the 1904-5 expedition that collected the holotype and paratype of *rothschildi*, A.S. Meek collected along the Dilava River and not the Aroa. Both the Dilava and the Aroa Rivers have their headwaters just south of Mt Tafa and both join about 10km from the coast. Heron argues that collections made at 'the head of the Aroa (= Dilava) River' would have been made at an altitude above 1200m which agrees with Tate's (1947) estimate of 'probably \pm 4000 feet'.

Apparently occurring between 600-1400m.

REPRODUCTION. Two lactating females were available (BBM 109489, BMNH 50.1110). The former, collected 13 March 1985, had 3 lactating nipples. Three well-grown, fully furred young were taken from the nest occupied by this female. The latter, collected 21 December 1940 was labelled 'with 2 embryos attached to the teats'. It is possible that the normal nipple number in *M. rothschildi* is 4, and that the 3 and 2 seen here result from small litters or are aberrant.

DESCRIPTION. *Mean Measurements* (mm). External: Total length (head, body, tail) TL (δ) 325 (η) 291; Hind Foot (δ) 27.25 (η) 26.50; Ear (notch) (δ) 20.13 (η) 19.50; Skull: basicranial length (δ) 36.78 (η) 31.31; M^{1-4} (δ) 8.85 (η) 8.29; M^2 width (δ) 2.46 (η) 2.40. (Table 5).

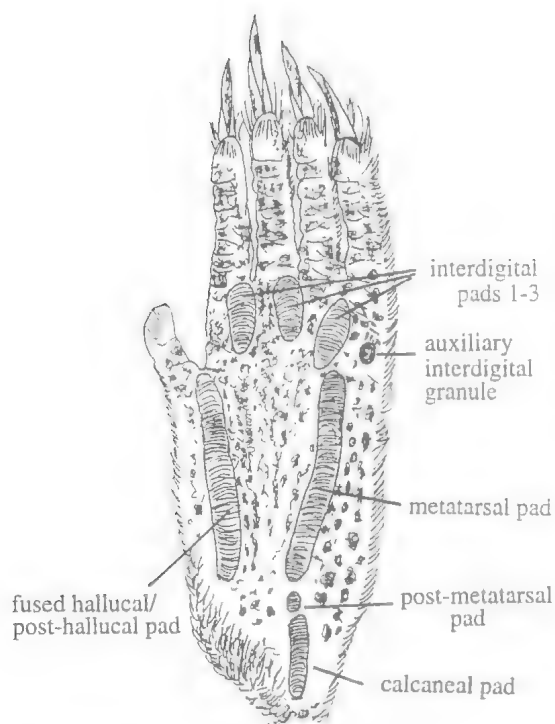


FIG. 33. Hindfoot padding in *Paramurexia rothschildi*.

Body Size. Although all but one ♂ (BMNH 50.1111) registered a basicranial length greater than that of the largest ♀, size difference between the sexes was not statistically significant ($t = 0.42$).

P₄ Morphology. Three juveniles were available for P⁴ assessment. In BBM 109485 both left and right P⁴ were single-rooted, broad and premolariform with 2 cusps, one prominent anterior, the other a very weak posterior. Strong lingual cingulation was present on both. Left and right P₄ were single-rooted and premolariform, with a prominent anterior cusp which broadened posteriorly into a flat shelf.

In BBM 109481 left and right P⁴ were single-rooted and more molariform than in BBM 190485. The metacone featured most prominently, but the paracone was present as a small, narrow spur. On both, styler cusp E was well developed. The right P₄ was single-rooted, broad and premolariform with a small anterior cusp and the posterior, flat and peg-like. LP₄ was not present. In BMNH 50.1110 a right P⁴ was present. Its morphology was similar to that of BBM 109485.

Hind Foot Morphology (Fig. 33). Unique for its extraordinary development of proximal pads of the hind foot. All specimens showed a greatly elongate metatarsal pad with close approximation to the third interdigital pad. Posterior to the metatarsal pad, a large striate postmetatarsal pad may be present (e.g., BBM 109841, BBM 109845, BBM 109489), or a small postmetatarsal pad may occur in close approximation with a very large striate calcaneal pad (e.g., AMNH 108106). All specimens examined exhibited an auxiliary pad outside the third interdigital pad of both left and right hind feet.

SPECIMENS EXAMINED. Agaun, 1km E. 1240m, 09°56'E 149°23'S (BBM 109481, BBM 109483, BBM 109485, BBM 109487); Agaun, 2.5km E., 1400m, 09°56'E 149°23'S (BBM 109489); Agaun at 4,500' (CM 12340); Aroa River (head of), 1220m, 08°57'E 147°00'S (BMNH 1939.3233, AMNH 108106); Boneno, 1220m, 09°54'E 149°25'S (BMNH 50.1111-12); Enaena, Mt Simpson, 1372m, 10°02'E 149°34'S (BMNH 50.1108-10); Ikara, Mt Simpson, 09°58'E 149°38'S (BMNH 50.1107); Opanabu (near Nowata), 610m, 10°01'S 149°43'E (CM 12287).

Murexechinus gen. nov.

Phascogale (in part), Temminck, 1824.

Antechinus (in part) Macleay, 1841.

TYPE AND ONLY SPECIES. *Phascogale melanura* Thomas, 1899.

GENERIC DIAGNOSIS. M¹ very broad, with wide protocone and complete anterior cingulum, the anterior margin of this tooth is straight or anteriorly convex, but not indented or concave. Tail longer than the head-body length.

It is distinguished from *Phascolosorex* and *Myoictis* by its lack of a dorsal body stripe and by its lack of reduced premolars, and from *Neophascogale* by its lack of reduced premolars and lack of a thickly-haired, white-tipped tail.

Murexechinus differs from *Micromurexia* as follows: ears with rich rufous to light fawn post-auricular patches rather than lacking post-auricular patches; pelage shows definite change in colour from head to rump (usually agouti changing to warm russet) rather than uniform colour throughout; claws are thick and strongly curved rather than semi-straight and thin; tail thickly haired a uniform black (sometimes dark brown) rather than thinly haired and dorsoventrally bicoloured; I¹ broad, claw-like and heavily crowned rather than narrow, needle-like and minutely crowned; I²⁻⁴ strongly cingulated buccally and lingually, blade-like and robust rather than uncingulated.

TABLE 5. Absolute measurements for *Paramurexia rothschildi*. See 'Methods' for limits of measured dimensions and Table 1 (caption) for abbreviations.

Measurement		N	mean±r	OR	SD	V	CV
BL	Male	6	36.78±1.15	32.03-40.49	2.82	7.96	7.67
	Female	2	31.31±1.30	29.48-33.14	1.83	3.35	5.84
	Total	8	35.41±1.25	29.48-40.49	3.53	12.43	9.97
ZW	M	6	21.97±0.69	18.86-23.86	1.68	2.81	7.65
	F	2	19.23±0.97	17.86-20.60	1.37	1.88	7.12
	T	8	21.29±0.71	17.86-23.86	2.00	3.99	9.39
IOW	M	6	7.61±0.13	7.22-8.18	0.32	0.10	4.20
	F	2	7.84±0.23	7.53-8.16	0.32	0.10	4.08
	T	8	7.67±0.12	7.22-8.18	0.33	0.11	4.30
OBW	M	6	13.49±0.34	12.24-14.69	0.84	0.71	6.23
	F	2	12.38±0.28	11.98-12.78	0.40	0.16	3.23
	T	8	13.21±0.32	11.98-14.69	0.90	0.80	6.81
IBW	M	6	7.48±0.24	6.40-8.15	0.58	0.34	7.75
	F	2	6.65±0.18	6.39-6.91	0.26	0.07	3.91
	T	8	7.27±0.22	6.39-8.15	0.63	0.40	8.67
R-LC ¹	M	6	7.56±0.24	6.26-8.09	0.60	0.36	7.94
	F	2	6.40±0.20	6.12-6.67	0.28	0.08	4.38
	T	8	7.72±0.26	6.12-8.09	0.74	0.55	9.59
R-LM ¹	M	6	12.59±0.24	11.35-13.10	0.58	0.34	4.61
	F	2	11.02±0.24	10.68-11.36	0.34	0.12	3.09
	T	8	12.20±0.31	10.68-13.10	0.87	0.75	7.13
R-LM ²	M	6	15.13±0.27	13.85-15.87	0.66	0.43	4.36
	F	2	13.79±0.15	13.58-14.00	0.21	0.04	1.52
	T	8	14.79±0.29	13.58-15.87	0.82	0.67	5.54
R-LM ³	M	6	18.08±0.39	16.34-19.39	0.96	0.92	5.31
	F	2	16.35±0.35	15.86-16.84	0.49	0.24	3.00
	T	8	17.65±0.40	15.86-19.39	1.14	1.31	6.46
R-LM ¹ T	M	6	10.29±0.23	9.40-11.32	0.56	0.32	5.44
	F	2	9.44±0.17	9.20-9.68	0.24	0.06	2.54
	T	8	10.08±0.22	9.20-11.32	0.62	0.39	6.15
I ¹ -M ⁴	M	6	20.25±0.44	18.38-21.66	1.09	1.18	5.38
	F	2	17.97±0.16	17.75-18.19	0.22	0.05	1.22
	T	8	19.68±0.48	17.75-21.66	1.37	1.87	6.96
P ¹⁻³	M	6	4.85±0.16	4.26-5.42	0.38	0.15	7.84
	F	2	4.51±0.21	4.21-4.80	0.30	0.09	6.65
	T	8	4.77±0.14	4.21-5.42	0.39	0.16	8.18
M ¹⁻⁴	M	6	8.85±0.13	8.47-9.27	0.31	0.10	3.50
	F	2	8.29±0.09	8.16-8.41	0.13	0.02	1.57
	T	8	8.71±0.13	8.16-9.27	0.37	0.14	4.25
M ² W	M	6	2.46±0.05	2.32-2.69	0.13	0.02	5.28
	F	2	2.40±0.01	2.39-2.41	0.01	0.00	0.42
	T	8	2.45±0.04	2.32-2.69	0.11	0.01	4.49
Dent	M	6	29.39±0.98	25.35-32.32	2.40	5.78	8.17
	F	2	25.15±0.96	23.80-26.49	1.35	1.81	5.37
	T	8	28.33±1.01	23.80-32.32	2.86	8.17	10.10
I ₁ -M ₄	M	6	17.86±0.29	16.91-18.79	0.72	0.52	4.03
	F	2	15.95±0.06	15.87-16.03	0.08	0.01	0.50
	T	8	17.39±0.37	15.87-18.79	1.04	1.08	5.98
P ₁₋₃	M	6	5.23±0.15	4.68-5.75	0.36	0.13	6.88
	F	2	4.40±0.23	4.07-4.73	0.33	0.11	7.50
	T	8	5.03±0.18	4.07-5.75	0.51	0.26	10.14
M ₁₋₄	M	6	9.56±0.07	9.29-9.70	0.18	0.03	1.88
	F	2	9.27±0.03	9.23-9.30	0.04	0.00	0.43
	T	8	9.48±0.07	9.23-9.76	0.20	0.04	2.11
M ₂ W	M	6	1.58±0.03	1.48-1.72	0.07	0.01	4.43
	F	2	1.48±0.01	1.46-1.50	0.02	0.00	1.35
	T	8	1.56±0.03	1.46-1.72	0.08	0.01	5.13
TL	M	5	325±9.85	295-350	22.03	485.32	6.78
	F	3	290.67±7.42	276-300	12.86	165.38	4.42
	T	8	312.63±9.05	276-350	25.60	655.36	8.19
T	M	4	172±4.50	162-184	9	90	5.23
	F	2	161±6.38	152-170	9	81	5.59
	T	6	168±4.08	152-184	10	112	5.95
HF	M	4	27.25±0.55	26-29	1.09	1.19	4.00
	F	2	26.50±1.06	25-28	1.50	2.25	5.66
	T	6	27.00±0.53	25-29	1.29	1.67	4.78
E	M	4	20.13±0.45	19-21.5	0.89	0.80	4.42
	F	2	19.50±0.35	19-20	0.50	0.25	2.56
	T	6	19.92±0.34	19-21.5	0.84	0.70	4.22
W	M	1	40				
	F	1	64				
	T	1	64				

narrow and lensate; $C^{1/1}$ short and thick rather than extremely long and slender; upper premolar row short, with premolars crowded, wide and robust rather than premolar row long with premolars uncrowded and narrow; P^1 and P^2 in close contact rather than separate; lower molars with weak entoconids (i.e., M_3 entoconid shorter than paraconid) rather than very well developed entoconids; nasals flat rather than raised and fluted.

Murexechinus differs from *Phascomurexia* as follows: ears with rich rufous to light fawn post-auricular patches rather than lacking post-auricular patches; pelage shows definite change in colour from head to rump (usually agouti changing to warm russet) rather than uniformly brown throughout; tail thickly haired a uniform black (sometimes dark brown) throughout, with ventral crest hairs long for entire tail length rather than semi-naked dorsally with weak ventral crest developing appreciably only toward distal end; I^1 broad and claw-like and heavily crowned rather than narrow and needle-like; I^{2-4} strongly cingulated rather than uncingulated; $C^{1/1}$ short and thick, rather than long and slender; premolar row short with premolars crowded and broad, rather than long premolar row with uncrowded narrow premolars; P^1 and P^2 in close contact rather than separate.

Murexechinus is separable from *Murexia* by the shorter length of its upper and lower premolar rows $P1-3$.

Murexechinus is separable from *Paramurexia* by its smaller ears. *M. melanurus* also lacks a dark longitudinal dorsal body stripe.

***Murexechinus melanurus* (Thomas, 1899)**
(Figs 34, 35, 36)

Phascogale melanura Thomas, 1899: 191.

Phascogale melanura modesta Thomas, 1912: 92.

Phascogale mayeri Dollman, 1930: 433, pl. 4.

Antechinus wilhelmina Tate, 1947: 130.

LECTOTYPE. CE 3915. Adult ♀ puppet skin, faded. Skull extracted but missing parietals, supraoccipitals and part of squamosal bones. PARALECTOTYPE. BMNH 1900.6.26.1, adult ♂ in ethanol, skull not extracted (lower jaw broken and skin badly faded).

TYPE LOCALITY. Moroka, headwaters of the Musgrave River, PNG, 9°24'S 147°32'E. At 1,300m. Coll L. Loria, 7 August 1893.

DIAGNOSIS. As for genus.

DESCRIPTION OF LECTOTYPE, PARALECTOTYPE AND DELEGATE. *Pelage* (Fig. 34). Both are very badly faded; lectotype is

overall a Buffy Brown on the shoulders which changes to Olive Brown over the rump. The belly is an overall Olive Buff and the tail is Olive Brown near the base, changing to Clove Brown nearer the tip. Post-auricular patches are a very faded Tawny Olive. There is no visible change in head to body colour. Paralectotype BMNH 0.6.26.1 (in ethanol) (Fig. 35) was not recorded for pelage colour.

To demonstrate typical colour patterns of *M. melanurus*, another specimen (AMNH 15704) has been selected (from a site as close as possible to the type locality) for pelage description. This will also serve as a basis upon which *A. wilhelmina* can be compared later. Little can be gained from a detailed pelage description of the lectotype and paralectotype.

AMNH 157074, adult ♂ study skin and skull, collected on Mt Dayman, Maneau Range (9°50'S 149°18'E): Fur above shoulders (6mm long) has basal 4mm Deep Mouse Gray, median 1mm Light Ochraceous Buff and apical 1mm black. The mid-back thereby appears a speckled agouti. Medially thickened guard hairs are interspersed thinly through the fur and are 8mm long on the rump and reduce to 3mm where they terminate at the crown of the head. Fur on the head is dominated by coarse black guard hairs giving the head a darker appearance than any other part of the body. Fur on, and above the shoulders, has a darkening of the median band to Ochraceous Tawny and black tips are gradually lost from guard hairs toward the sides of the body, leaving the mid-sides a soft Buckthorn Brown. There is no head-stripe or eye-ring.

A band of short, black, eyelash hairs completely encircles the eye. Coarse hairs (5.5mm long) around the anterior rim of the ear have expanded the pigmented median band to 2mm (Ochraceous Orange) giving a vague pre-auricular patch. Hairs immediately behind the ear have scarcely visible black tips but coarse guard hairs are absent. These soft hairs are coloured Ochraceous Orange and create a spectacular, soft post-auricular patch. From mid-shoulders to the rump the median colour band of hairs changes gradually from Light Ochraceous Buff through to Ochraceous Orange giving the rump, thighs and base of the tail a warm Ochraceous Tawny colour. The soft ventral fur (6.5mm long on the belly and 5mm long on the interramal region) is Light Mouse gray on the basal half and Warm Buff on the apical half and is interspersed by Warm Buff medially thickened

guard hairs 5mm long. The mid-belly is thus an overall Warm Buff.

Forefeet are covered thinly with Warm Buff hairs. Hindfeet are more thickly covered with darker Ochraceous Buff hairs. The tail is darkly coloured with Fuscous Black hairs averaging 2.5mm along its dorsal length and increasing to 3.5mm at the tip. Ventrally the hairs increase in length from 4mm at the base to 7mm at the tip giving a ventral crest which is slightly lighter (Clove Brown) than the dorsal surface.

Vibrissae (lectotype). Approximately 21 mystaceal vibrissae occur on each side and are up to 27mm long. The more dorsal mystaceal vibrissae are Fuscous Black while those lower have colourless tips. Supra-orbital vibrissae (Fuscous Black) number 2 (left) and 2 (right); genals (Fuscous Black and colourless) number 6 (left) and 6 (right), ulna-carpals (colourless) number 4 each side; submentals (colourless) number 3.

Tail (lectotype). The tail is much longer than head and body. It is thin and tapers toward the tip.

Hindfoot (lectotype). Interdigital pads are separate. The apical granule is greatly enlarged, elongate and striate. Hallucal and posthallucal pads are joined. The metatarsal pad is greatly enlarged, striate and extends forward almost touching the third interdigital pad.

Ears (lectotype). Pinnae are large with a complex supratragus which has a pronounced thickened posterior margin. The distal end is reflected ventrally. The reflected tip is slightly concave.

Dentition (lectotype) (Fig. 36). Upper Incisors: I^1 is broad, heavy and claw-like, procumbent and sharply curved posteriorly. It is taller crowned than all other upper incisors and is separated from I^2 by a diastema. Left and right I^1 are widely separate at their roots but the teeth touch almost halfway up the crown then to diverge away from each another. For I^{2-4} crown height and width, I^2 is greater than I^3 which is greater than I^4 . All upper incisors show distinct buccal cingula but I^1 carries no anterior or posterior cusps. Roots of I^1 are narrow.

Upper Canines: C^1 is heavy and caniniform with very weak buccal and lingual cingula. A minute posterior cusp is present.

Upper Premolars: No diastemata occur in the premolar row which is short and crowded and characterised by the broad, heavy premolars. All carry strong buccal and weaker lingual cingula. P^1 is shorter than P^2 which is shorter than P^3 . No clearly definable anterior or posterior cusps

occur on the upper premolars. P^1 is very broad with slight postero-lingual lobing, P^2 is broad, LP^3 is crushed obliquely between P^2 and M^1 , RP^3 is missing in the lectotype skull.

Upper Molars: The posterior tip of P^3 is outside and slightly buccal to the parastylar corner of M^1 . The anterior cingulum below stylar cusp B is very short and broad but complete. Stylar cusp B is unworn and reduced, and a minute protoconule is present at the base of the paracone apex. The paracone on M^1 is approximately half the length of the metacone. Stylar cusps C and E are not present in R or LM^1 . M^1 has a strong posterior cingulum. There is an (?) abnormal spur of enamel directly below the preprotocrista. Stylar cusp D is reduced and narrow.

In M^2 a very broad anterior cingulum contacts the metastylar corner of M^1 , tapers slowly as it progresses down and along the base of the paracrista and finally expands into the trigon basin. No protoconule is present. Stylar cusp D is high and narrow and there is a strong posterior cingulum. M^2 lacks stylar cusps A, C and E.

In M^3 the anterior cingulum is broad, strong and complete, as in M^2 . Stylar cusp D is greatly reduced to a very small sharp peak. Stylar cusps E and C are absent as is the protoconule.

In M^4 the metastylar corner is weakly developed. The basal anterior cingulum is complete but narrower than in M^3 . A posterior cingulum is weakly present. The protocone is broad but short. In occlusal view the angle made between the post-paracrista and the post-protocrista is 135° , indicating no metacone development.

Lower Incisors: The first lower incisor is much greater in crown height than I_2 . I_1 and I_2 are oval in anterolateral view and gouge-like in occlusal view. I_2 is subequal in crown height to I_3 but narrower than I_3 . I_3 is incisiform in lateral view with an inconspicuous posterior cusp at the base of the crest which descends posteriorly from the apex of the primary cusp. The lower canine rests against this posterior cusp. In occlusal view a gross notch separates this posterior cusp from the prominent posterolingual lobe.

Lower Canines: C_1 is short, heavy, broad and caniniform and characterised by forward projection and slight curvature from root to crown. It has very weak buccal but strong lingual cingulation and a very weak cingular cusp.

Lower Premolars: The lower premolar row is short and crowded and P_{1-3} are broad and crushed, strongly cingulated buccally and lingually. In

crown height P_4 is taller than P_3 which is taller than P_1 . All premolars are very broad and triangular. All possess small broad posterior cusps though none possesses an anterior cusp. P_4 is set very low as if not fully erupted. The bulk of each premolar mass is concentrated posterior to the line drawn transversely through the middle of the two premolar roots. P_1 is heavily lobed posterolingually.

Lower Molars: All the molars are broad and the molar row is relatively short. The M_1 talonid is much wider than the trigonid and an anterior cingulum is present but poorly developed. It terminates at the posterior base of the protoconid. A buccal cingulum is present. The M_1 paraconid is scarcely developed and appears in occlusal view as a minute spur, the lingual edge of which makes almost no appreciable swelling on the endoloph of M_1 . The hypoconid and metaconid are roughly oblique to the long axis of the dentary. The cristid obliqua is long and extends from the hypoconid to the posterior wall of the trigonid intersecting the trigonid at a point slightly lingual to that point directly below the tip of the protoconid. The entoconid is high, long and blade-like. From the base of the metaconid posteriorly the talonid endoloph bulges lingually but returns with a buccal orientation to the hypoconulid.

In M_2 the talonid is slightly wider than the trigonid. The anterior cingulum is very well developed originating buccally in a weak parastylid notch into which the hypoconulid of M_1 is tucked. The buccal cingulum is strongly developed from the base of the protoconid to amalgamate with the posterior cingulum. The paraconid is well developed and is the smallest trigonid cusp. There is a minute metastylid and the entoconid is low but long. The cristid obliqua intersects the trigonid directly below the tip of the protoconid but well buccal to the metaconid fissure. The hypoconid extends from slightly anterior and buccal to the hypoconulid to the tip of the hypoconid. The endoloph of the trigonid follows the line of the dentary with no input from the entoconid.

In M_3 the trigonid is wider than the talonid. A small parastylid wraps around the hypoconulid of M_2 and there is a very strong anterior cingulum which terminates at the anterior base of the paraconid. Buccal and posterior cingula are as in M_2 but more poorly developed. The reduced cristid obliqua intersects the trigonid at a point well lingual to the longitudinal vertical midline drawn through the tip of the protoconid but

slightly buccal to the metaconid fissure. There is a low, poorly developed entoconid on M_3 . The talonid endoloph makes a more buccal swing than that seen in M_2 . Both the metaconid and hypoconid are oblique to the long axis of the dentary.

In M_4 the trigonid is wider than the talonid. The anterior cingulum is as in M_2 . The posterior cingulum is weakly present. Of the three main trigonid cusps, the metaconid is slightly taller than the paraconid but both are dwarfed by the protoconid. A true hypoconid on M_4 is absent. Between the pseudo-hypoconid and the base of the metaconid, the cristid obliqua forms a very low, weak crest which degenerates before contacting the trigonid wall. A significant feature of M_4 morphology is the reduction of talonid crown enamel below the cristid obliqua (which could be regarded as M_4 buccal cingulum) which results in the talonid appearing (in occlusal view) as a narrow unsupported spur jutting off the trigonid wall. There is no entoconid on M_4 .

Skull (Fig. 36). *M. melanurus* is a broad-faced dasyurid with a conspicuous concavity at the junction of the nasal and frontal bones, just anterior to the interorbital region. In the lectotype, the parietal, supraoccipital and part of the squamosal bones are missing and no fluting or inflation of the nasal bones is detectable. The left and right alisphenoid tympanic bullae are widely separated and very small. The foramen pseudovalve is very large and not bisected by the inner wing of the entocarotid canal. The eustachian canal opening is large, the posterior lacerate foramina are small and protected by a flange of the wing of the petrosal part of the petrotic. The premaxillary vacuity extends from the level of the I^2 root back to the level of the edge of the anterior root of P^1 . The small maxillary vacuities extend from the level of the protocone root of M^1 back to the level of the metastylar corner of M^2 . Palatine vacuities are absent.

SYNONYMS

Phascogale melanura modesta Thomas, 1912
(Fig. 37)

HOLOTYPE. BMNH 10.11.29.11, adult σ (shagbilly tailed skin, no skull in existence).

TYPE LOCALITY. Mt Goliath, Irian Jaya, 4°43'S 139°52'E. Coll. A.S. Meek.

ALTITUDE. Not quoted in type description (Tate, 1947 quotes 'from about 5,000 feet', [1,525m]).

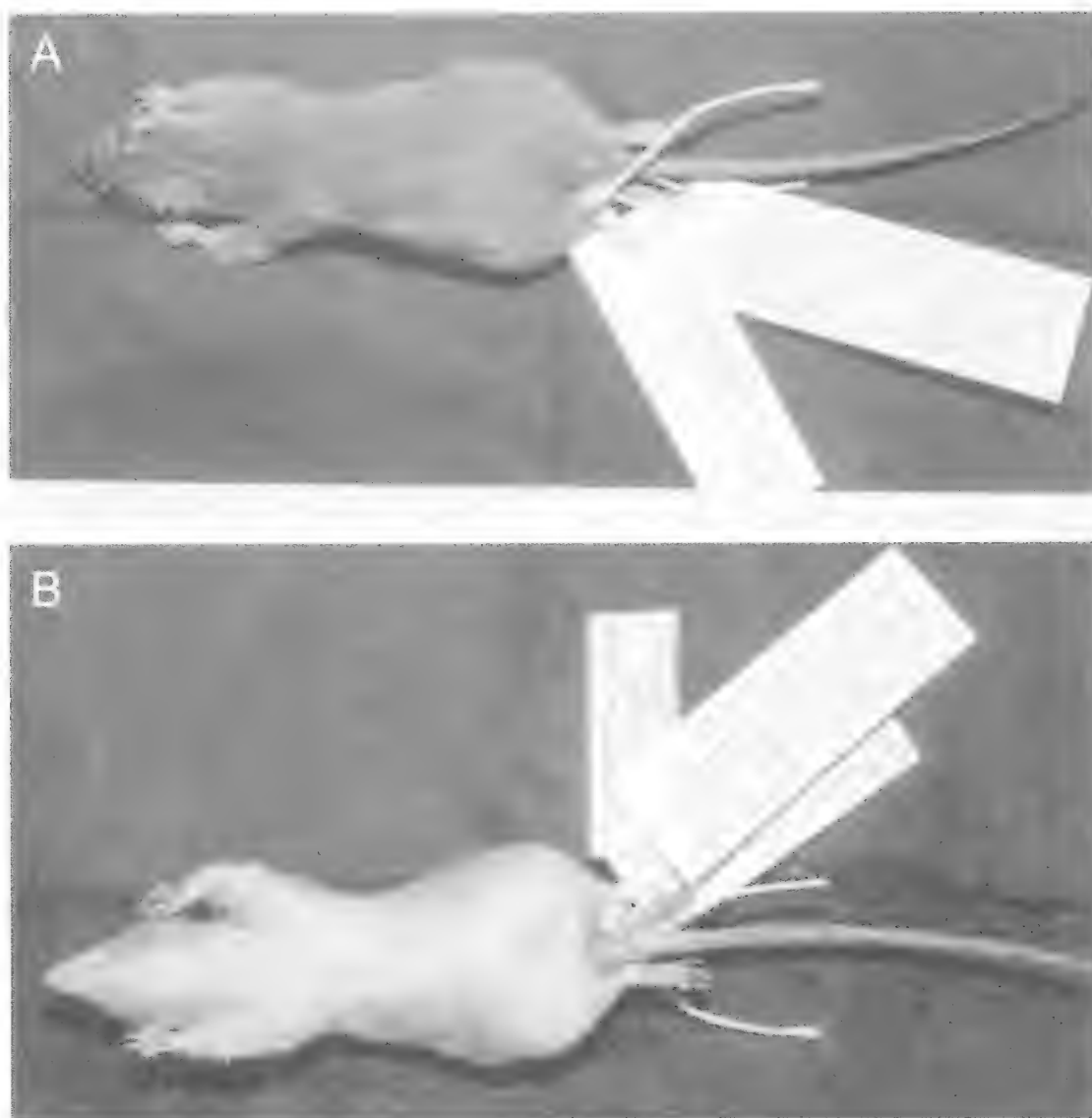


FIG. 34. Lectotype of *Phascogale melanura* Thomas, 1899 (now *Murexechinus melanurus*). CE 3915, study skin: A, dorsal view; B, ventral view. TL = 234mm; HB = 106mm; TV = 128mm; HF = 20mm.

DESCRIPTION. *Pelage* (Fig. 37). The skin shows a very small, relatively drab-looking animal with slipped belly fur and missing left fore-leg. The degree of fading is unassessable. Head colour is Sepia, mid-back Saccardo's Umber, rump Olive Brown. The thinly-haired tail is Bone Brown dorsally and Olive Brown ventrally. Dorsal manus and pes are Buffy Brown. The belly is Grayish Olive. Post-auricular patches are coloured Tawny Olive. Other external features are as in the lectotype.

Skull and Dentition. A skull does not accompany the study skin.

Phascogale mayeri Dollman, 1930
(Figs 38, 39)

HOLOTYPE. BMNH 29.5.27.57 (on label accompanying specimen), 'BM 29.5.37.57' (quoted in original description). Adult ♀ (skin and skull in good condition).

TYPE LOCALITY. Arfak Mountains, Irian Jaya, 1°09'S 134°00'E. At 1,000m. Coll. F. Shaw Mayer, 22 August 1921.



FIG. 35. Paralectotype of *Phascogale melanura* Thomas, 1899 (now *Murexechinus melanurus*). BMNH 1900.6.26.1, lateral view of alcoholic body. TL = 227mm; HB = 107mm; TV = 120mm; HF = 21mm.

DESCRIPTION. *Pelage* (Fig. 38). Typically drab representatives of the species at the western end of Irian Jaya. Head colour to mid-back is Sepia which warms on the rump, base of hind legs and tail to a Bister. Post-auricular patches are a dull Cinnamon Buff. The tail is well haired, and uniformly dark Olivaceous Black dorsally and Chaetura Drab ventrally. The overall impression of the dorsal pelage is of a dull agouti (green-brown with golden flecks) warming to a deeper brown-orange on the rump. The belly in *P. mayeri* is a very light Pale-Olive Buff and the fore and hind feet are Hair Brown. Other external features are as in the lectotype.

Dentition (Fig. 39). There are very few features in *P. mayeri* which differ from the lectotype dentition. *P. mayeri* teeth are heavily worn and RI^1 is lost as in RP_1 . It is significant that crown height in incisor I^1 is greater than I^2 which is sub equal to I^2 . There are clear, complete cingula on M_1 .

Antechinus wilhelmina Tate, 1947
(Figs 40, 41)

HOLOTYPE. AMNH 109811, adult ♂ (skin and skull in excellent condition).

TYPE LOCALITY. 9km NE of Lake Habbema, Mt Wilhelmnia, Irian Jaya. 4°05'S 138°50'E. At 2,800m. Coll. W.B. Richardson, 19 October 1938.

DESCRIPTION. *Pelage* (Fig. 40). Representative of the typically drab individuals of *melanurus* of Irian Jaya, but shows the very small size of adult animals from higher altitudes. The striking back tones seen in eastern animals are replaced with more sombre tones so that the

head and tail are a muddy brown and post-auricular patches are unimpressive buff tones. With the strength of black in fur tips reduced throughout, the head and mid-back appear as a flecked Tawny Olive, the rump as a slightly warmer Saccardo's Umber, the tail a dull Bister. The belly is a Pale Cinnamon Pink (a dirty white) and post-auricular patches Cinnamon Buff.

Dentition (Fig. 41). I^1 is reasonably broad and slightly procumbent. It is a small replica of the typical broad, claw-like I^1 of *M. melanurus* where crown height $I^2 = I^1$ which is greater than I^1 . C^1 is heavy and caniniform but lacks anterior and posterior cusps and buccal and lingual cingula, while the upper premolar row is short and crowded with no space separating the premolars. The premolars are more oval in occlusal view than in larger specimens. In M^1 stylar cusp B is greatly reduced and the preparamacrista is extremely short. There is no protoconule. In M^2 and M^3 stylar cusp C is visible. There is no development of a metacone on M^4 . The lower premolar row is short and crowded and is characterised by broad, rectangular P_1 and P_2 . Premolars contact or are closely approximated. In M_1 the paraconid is broader than in the lectotype of *P. melanura*. It appears as a broad flat spur, the lingual edge of which makes an appreciable swelling on the endoloph of M_1 . Entoconids are reduced throughout.

Skull (Fig. 41). The skull lacks a concave depression at the nasal-frontal suture.

ADDITIONAL DIAGNOSTIC FEATURES

Murexechinus differs from all other dasyurids in: I , I^1 only slightly procumbent but robustly



FIG. 36. Lectotype of *Phascogale melanura* Thomas, 1899. CE 3915, cranium and dentary. Sex = f; BL = 26.75; ZW = 16.73; IO = 6.93; OBW = 11.24; IBW = 5.52; R-LC¹ = 5.41; R-LM¹ = 9.81; R-LM² = 12.32; R-LM³ = 14.47; R-LM⁴T = -; M²W = 2.13; I¹-M⁴ = 14.69; P¹⁻³ = 3.19; M¹⁻⁴ = 6.85; Dent = 21.25; I₁-M₄ = -; P₁₋₃ = 3.28; M₁₋₄ = 7.46; M₂W = 1.37.

built, curved (claw-like), laterally compressed with much heavier crown and lower cingulum than *Micromurexia*, *Murexia*, *Phascomurexia* or *Paramurexia*; 2, I¹ and I² widely separated; 3, cingulated upper incisor row of broad-crowned teeth. Unlike in *Micromurexia*, *Murexia*, *Phascomurexia* and *Paramurexia*, I²=I³=I⁴ and sometimes I²>I³>I⁴; 4, I⁴ without a posterior cusp; 5, upper canines heavier and shorter than in *Micromurexia*, *Paramurexia*, and *Murexia*, but similar to *Paramurexia*. There is no posterior cusp; 6, an upper premolar row in which the more heavily cingulated teeth are uncrowded from C¹ to P², but where P³ may touch P² and M¹; 7, P¹ are

P² are rounded and show slight postero-lingual lobing and there is no posterior cusp on P³; 8, M¹ very broad, with wide protocone and complete anterior cingulum, the anterior margin of this tooth is straight or anteriorly convex, but not indented or concave; 9, M¹ and M² stylar cusp B large (smaller than stylar cusp D in M¹, subequal in M²); 10, M⁴ protocone more narrow than in *Micromurexia* but similar to *Paramurexia*, with anterior cingulum complete; 11, M¹ and M² stylar cusp D with tendency to be more conical than the low crest seen in *Micromurexia*, *Murexia* and *Phascomurexia*; 12, M⁴ metacone reduced more than in *Micromurexia*, *Phascomurexia*, and

Murexia, similar to condition in *Paramurexia*; 13, M^3 ectoloph more heavily indented than in *Micromurexia*, *Murexia*, *Phascomurexia* or *Paramurexia*; 14, moderately heavily cingulated lower premolar row in which the rounded teeth are slightly crushed, and where P_3 is smaller than P_2 ; 15, cingulated P_3 ; 16, M_3 talonid subequal to the trigonid width; 17, paraconid on M_1 more reduced than in *Micromurexia*, *Phascomurexia* and *Murexia*, but similar reduction to that seen in *Paramurexia*; 18, three very reduced cusps on the M_4 talonid; 19, entoconid is more reduced than in *Micromurexia*, *Phascomurexia* and *Murexia* on M_2 , similar reduction to that in *Paramurexia*; 20, metacristids and hypocristids are not transverse to the long axis of the dentary; 21, skull only slightly elongate and domed; 22, lightly fluted nasals; 23, poorly developed tympanic wing of the alisphoid with contrasting broad expansion of the pars mastoidea and adjacent squamosal; 24, tail thickly haired a uniform black (sometimes dark brown) throughout, with ventral crest hairs long for entire tail length; 25, polyoestrous and nipple number low (4); 26, penile morphology is simple.

In addition to those features noted in the generic diagnosis *M. melanurus* differs significantly ($P < 0.001$) from *Micromurexia habbema* as follows (measurements are means, mm): broader zygomatic ZW (16.89:15.56); narrower interorbital width IOW (7.09:7.62); wider outside bullae OBW (10.99:10.42); wider inside bullae IBW (5.12:4.72); wider rostrum R-LC¹ (5.43:5.00), R-LM¹ (9.71:8.03), R-LM² (11.91:10.49), R-LM³ (14.12:12.76); shorter upper premolar row P^{1-3} (3.37:3.85); longer upper molar row M^{1-4} (6.78:6.38); wider upper second molar M^2W (1.89:1.73); shorter lower premolar row P_{1-3} (3.45:4.08); longer lower molar row M_{1-4} (7.37:6.86); wider lower second molar M_2W (1.22:1.11); shorter ear E (15.83:16.95); post-hallucal and hallucal pads of hind foot always fused, without accompanying auxiliary apical granules rather than the usual unfused hallucal and posthallucal pads, with accompanying auxiliary granules.

M. melanurus also differs significantly ($P < 0.001$) from *Phascomurexia naso* as follows: shorter basicranium BL (26.83:30.13); narrower interorbital width IOW (7.09:7.66); narrower inside bullae IBW (5.12:5.81); narrower rostrum R-LM¹ (9.71:10.57), R-LM² (11.91:12.97), R-LM³ (14.12:15.48); narrower maxillae R-LM¹T (7.69:8.50); shorter upper tooth row I^1-M^4 (14.88:17.32); shorter upper premolar row

P^{1-3} (3.37:4.63); shorter upper molar row M^{1-4} (6.78:7.61); narrower second upper molar M^2W (1.89:2.02); shorter dentary Dent (21.31:24.23); shorter lower tooth row I_1-M_4 (12.96:15.18); shorter lower premolar row P_{1-3} (3.45:4.73); shorter lower molar row M_{1-4} (7.37:8.32); narrower lower second molar M_2W (1.22:1.31); shorter total TL (247:275); shorter tail T (133:149); shorter hind foot HF (22.27:25.35); shorter ear E (15.83:18.40); tail usually black and never with white tip, rather than light coloured and often with white tip.

M. melanurus differs significantly ($P < 0.001$) from *Murexia longicaudata* as follows: shorter basicranium BL (26.83:43.64); narrower zygomatic width ZW (16.89:25.33); narrower interorbital width IOW (7.09:7.81); narrower basicranium outside bullae OBW (10.99:14.59); narrower inside bullae IBW (5.12:8.44); narrower rostrum R-LC¹ (5.43:8.40), R-LM¹ (9.71:14.71), R-LM² (11.91:17.80), R-LM³ (14.12:21.24); narrower maxillae R-LM¹T (7.69:11.95); shorter upper tooth row I^1-M^4 (14.88:25.01); shorter upper molar row M^{1-4} (6.78:7.49); narrower upper second molar M^2W (1.89:2.75); shorter dentary length Dent (21.31:36.17); shorter lower tooth row I_1-M_4 (12.96:22.73); shorter lower molar row M_{1-4} (7.37:10.90); narrower lower second molar width M_2W (1.22:1.71); shorter total TL (247:398); shorter tail T (133:197); shorter hind foot HF (22.27:35.22); shorter ear E (15.83:20.50); ears with post-auricular patches rather than always lacking ear patches; pelage shows definite change in colour from head to rump (usually agouti changing to warm russet) rather than uniformly brown throughout; pelage long and soft rather than short and harsh, tail thickly haired a uniform black (sometimes dark brown) with ventral crest hairs long through entire length, rather than tail almost naked brown with very weak ventral crest developing toward the distal end; I^1 broad and claw-like rather than narrow and needle-like; in overall crown size I^2 is greater than or equal to I^3 which is greater than or equal to I^4 , rather than I^2 less than I^3 which is less than I^4 ; C^1/I_1 is short and stout; premolar row short with premolars crowded and broad, rather than premolar row with uncrowded, narrow, widely spaced premolars; rostrum short and broad rather than elongate; nasals flat rather than raised and fluted.

M. melanurus differs significantly ($P < 0.001$) from *Paramurexia rothschildi* as follows: Shorter basicranium BL (26.83:35.41); narrower

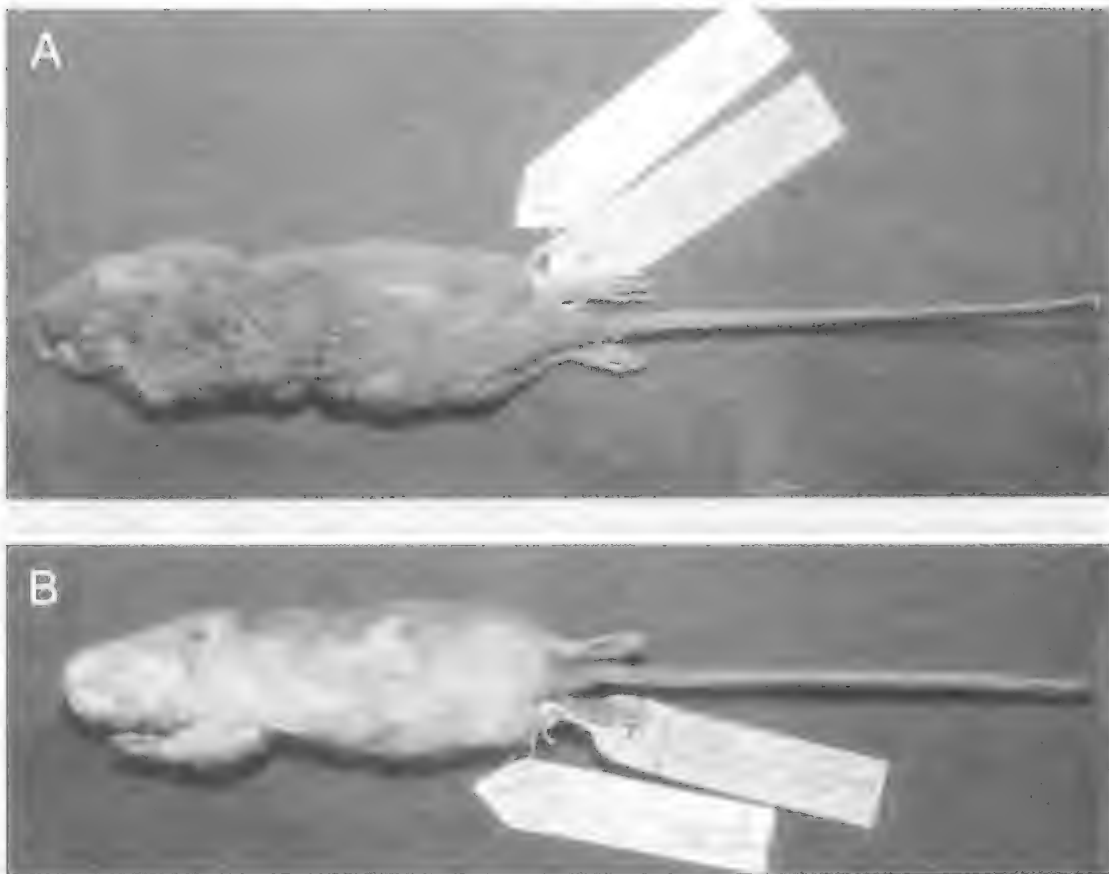


FIG. 37. Holotype of *Phascogale melanura modesta* Thomas, 1912 (now *Murexechinus melanurus*). BMNH 11.11.29.11, study skin; A, dorsal view; B, ventral view. TL = 232mm; HB = 106mm; TV = 126mm; HF = 20mm.

zygomatic width ZW (16.89:21.29); narrower basicranium outside bullae OBW (10.99:13.21); narrower inside bullae IBW (5.12: 7.27); narrower rostrum R-LC¹ (5.43: 7.72), R-LM¹ (9.71: 12.20), R-LM² (11.91: 14.79), R-LM³ (14.12: 17.65); narrower maxillae R-LM¹T (7.69:10.08); shorter upper tooth row I¹-M⁴ (14.88:19.68); shorter upper premolar row P¹⁻³ (3.37:4.77); shorter upper molar row M¹⁻⁴ (6.78:8.71); narrower upper second molar M²W (1.89:2.45); shorter dentary Dent (21.31:28.33); shorter lower tooth row I₁-M₄ (12.96:17.39); shorter lower premolar row P₁₋₃ (3.45:5.03); shorter lower molar row M₁₋₄ (7.37:9.48); narrower lower second molar M₂W (1.22:1.56); ears with post-auricular patches rather than a black mask; pelage shows a warming colour change toward the rump, rather than a dorsal longitudinal stripe; tail thickly haired a uniform black (sometimes dark brown) with ventral crest

hairs long throughout entire length, rather than tail thinly haired with short hairs and weak, lighter coloured ventral crest developing at the distal end.

REMARKS. *Taxonomic History.* *Murexechinus melanurus*, like no other species of New Guinean 'antechinus' has stood the test of time since its original description by Thomas in 1899. But it is not only its taxonomic longevity for which it is unique; it is unrivalled for its extraordinary range in colour, distribution and size. These factors have all contributed to the tangled fabric of its taxonomic history.

The original description was based on syntypes in Genoa and London, van der Feen, 1962 designated a lectotype. Later Thomas (1912), impressed by lack of bright auricular patches in an Irian Jayan specimen, proposed *P. melanura modesta*. While Thomas had few other spec-

imens to compare, later collections revealed specimens from the W which were drabber than *modesta* by the same degree that *modesta* was drabber than the nominate form; and specimens in the E which were more brightly coloured.

In 1930 Dollman (not 'Rothschild & Dollman', Tate 1947: 129) described a large, paler specimen from the far northwest of Irian Jaya (Arfak Mountains) which was later to be the bane of New Guinea dasyurid taxonomy. *Phascogale mayeri* was described for its large size and light colour, and Dollman was quick to point out its close affinity with *melanura* though it is doubtful that Dollman compared the skull of *mayeri* with the types of *melanura* despite his comments '... skull larger and more heavily built than in *P. melanura* ...' (Dollman, 1930: 433). In The Natural History Museum, London, Dollman had access to only three or four specimens of *melanura*; a small, subadult male collected by N.S. Meek from the Aroa River, a specimen collected by W. Stalker from the Marribore River, and Thomas' two types, *melanura* and *melanura modesta*. The study skin of *melanura modesta* was never accompanied by a skull and the paralectotype had never had the skull removed (it is still in the body today). Unless Dollman had access to the lectotype it is probably fair to assume that Dollman's comparison was based on the 5 cranial and dental measurements provided by Thomas in his *melanura* description.

With little British Museum comparative material (where the paralectotype of *melanura* and specimens of Meek and Stalker were relatively brightly coloured, and where the type of *melanura modesta* was such a small adult), it is not surprising that Dollman chose to label as *mayeri* a new series of large, brownish coloured animals with light-orange post-auricular patches collected by F. Shaw Mayer in the Weyland Range, Irian Jaya.

This decision however, led to the eventual undoing of *mayeri*. One of the specimens of this Weyland Range series, identified by Dollman as *mayeri*, eventually found its way into the Archbold Collection of the American Museum of Natural History (AMNH 101978) where Tate noticed that dental, cranial and external features were similar to his series of *melanura*. In 1937, Tate formalised his suspicions surrounding the identity of *mayeri* by reducing it to subspecific status as *Phascogale (Antechinus) melanurus mayeri*, 'the close likeness of both skin and skull

of *mayeri* to *melanura* is undeniable' (Tate 1937: 339).

During the decade following 1937, New Guinean specimens collected by F. Shaw Mayer and W. B. Richardson greatly enhanced the marsupial holdings of the British and American Museums of Natural History. Tate took advantage of this swelling comparative collection and, after examining type material in major European museums, made significant revision (1947) to the taxonomy of *melanurus* (as it was then). He retreated from his earlier assertion that *mayeri* was but a subspecies of *melanurus* and instead assigned Dollman's *mayeri* full specific status as the senior synonym of his and Archbold's *tafa* (= *naso*).

Reasons for this backtrack are inexplicable, especially when *mayeri* fulfilled all the criteria (dental, cranial and external) nominated by Tate himself (1947: 128) to diagnose specimens of *A. melanurus* (the skull of *mayeri* displayed the typically thick, heavy, first upper incisor, broad I²⁻⁴ and small palatal foramina, and the skin showed the bases of the ears coloured chestnut (to a reduced degree). The tail was black. These features never appeared in any of Tate & Archbold's *P. tafa* types or in any of the series associated with them). While, in retrospect, there was little justification in Tate's erecting separate subspecies for *centralis*, *tafa* and *misim*, it is little wonder that the subspecies *mayeri mayeri* had to exist to accommodate this one specimen (from unusually low altitude (1,000m) and with rufous ear-patches) about which Tate still felt uncomfortable, 'A good series is needed for comparison with *centralis*' (1947: 129). Even more pessimism regarding the future of the *mayeri* group was expressed by Tate, 'All four of these races stand so close to one another that later reviewers may decide that they should be merged together' (Tate 1947: 129). Despite this prediction, the epithet *mayeri* has been persistently and erroneously included with the *tafa*, *centralis*, *misim* group (= *naso*) e.g., Laurie (1952), Ziegler (1977), Van Dyck (1982a), Archer (1982a). Jenkins & Knutson (1983) assigned the *mayeri* holotype to *naso*.

Regarding the synonymy of *modestus*, Tate (1947: 128) summarised the characteristics of his three proposed groups of *Antechinus* in New Guinea and included *modestus* not in Group 1 with *melanurus* but in group 2 with *tafa*, *tafa centralis* and *mayeri* (group 3 was *wilhelmina*). The following page (p. 129) saw Tate

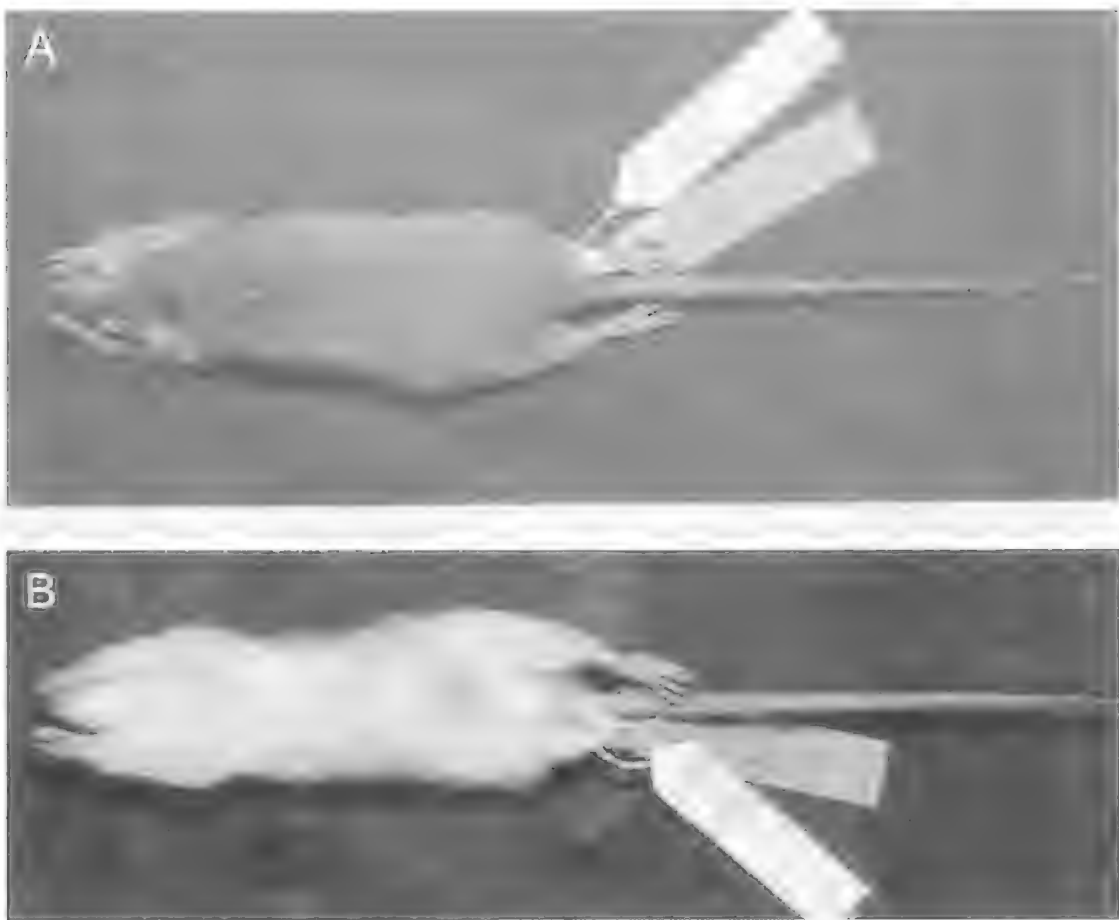


FIG. 38. Holotype of *Phascogale mayeri* Dollman, 1930 (now *Murexechinus melanurus*) BMNH 29.5.27.57, study skin; A, dorsal view; B, ventral view. TL = 259mm; HB = 116mm; TV = 143mm; HF = 23mm.

synonymise *modestus* with Thomas' *melanurus* (i.e., back to group 1). The reason for this is inexplicable (though some suggestions are made under 'Taxonomic History' in the account of *naso*).

Tate (1947) proposed *wilhelmina* to cater for not only the 'small replica(s) of *melanurus*' (p. 130) but to act as a sponge for what he considered an inadvertant taxonomic blunder associated with an earlier named species *habbema* (Tate & Archbold, 1941). The 'blunder' and its implications are discussed in detail under 'Taxonomic History' in the account of *habbema* and will only be summarised here.

Tate considered that *habbema* had been described from a mismatched skin and skull. In rectifying the problem he proposed to restrict use of the name *habbema* to the skin of the type

(which be considered to be an example of *mayeri* (= *naso*) and the skull he considered to be identical with another species which he named *wilhelmina* (= *melanurus*). The argument presented earlier here concludes that no mismatch had occurred and that the epithet *habbema* should still apply to the small, primitive, high-altitude dasyurid which constitutes the third and final New Guinea 'antechinus' after *naso* and *melanurus*. The type of *wilhelmina* represents no more than that which Tate had originally described it as 'a small replica of *melanurus*' (p. 130), and a junior synonym of that species.

Characters Tate then ascribed to *wilhelmina* became a composite of the characters of two different species which Tate considered the same. 'Furthermore the skull which was associated with

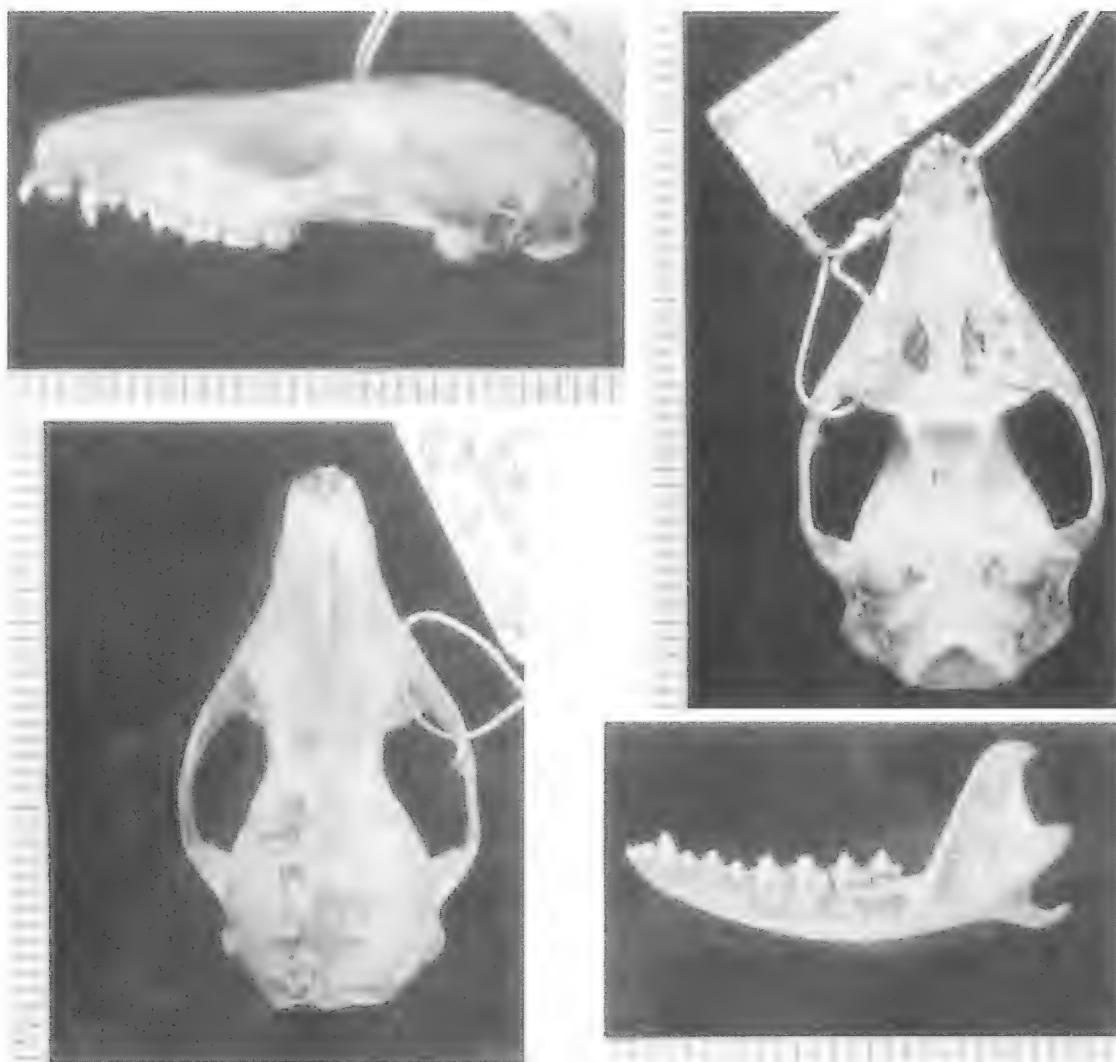


FIG. 39. Holotype of *Phascogale mayeri* Dollman, 1930, BMNH 29.5.27.57, cranium and dentary. Sex = f; BL = 30.12; ZW = 18.44; IO = 6.86; OBW = 11.79; IBW = 5.97; R-LC¹ = 6.28; R-LM¹ = 11.17; R-LM² = 13.66; R-LM³ = 15.78; R-LM¹T = 8.85; M²W = 2.15; I¹-M⁴ = 16.81; P¹⁻³ = 4.05; M¹⁻⁴ = 7.41; Dent = 24.53; I₁-M₄ = 14.28; P₁₋₃ = 4.08; M₁₋₄ = 8.29; M₂W = 1.37.

the type skin of *A. habbema* exactly matches the skulls of *wilhelmina*' (Tate 1947: 131)! For example, features noted for *wilhelmina* included: 'bases of the ears faintly chestnut; tail black above and below. Body color gray brown, the hairs strongly washed with rufous' (all features of *melanurus*), '... first incisors very slender, other incisors narrow and slender; premolars small' (all features of *M. habbema*) '... mp⁴ single-rooted' (a variable feature of *M. melanurus*) '... molars very small' p.128 (a *habbema* feature).

Laurie (1952) diagnosed the significance of a series of specimens from Mt Tomba, NE PNG (Shaw Mayer, 1947). She drew attention to basic differences from *wilhelmina* — their uniform brownish grey body colour, the rump not contrastingly reddish, the lack of ear patches, the tail being brown above and pale buffy below, and she described the species as *A. hageni* (= *habbema*). However, two years later she synonymised her *A. hageni* with the very species (*wilhelmina*) in which she had previously recognised so many conflicting characters.

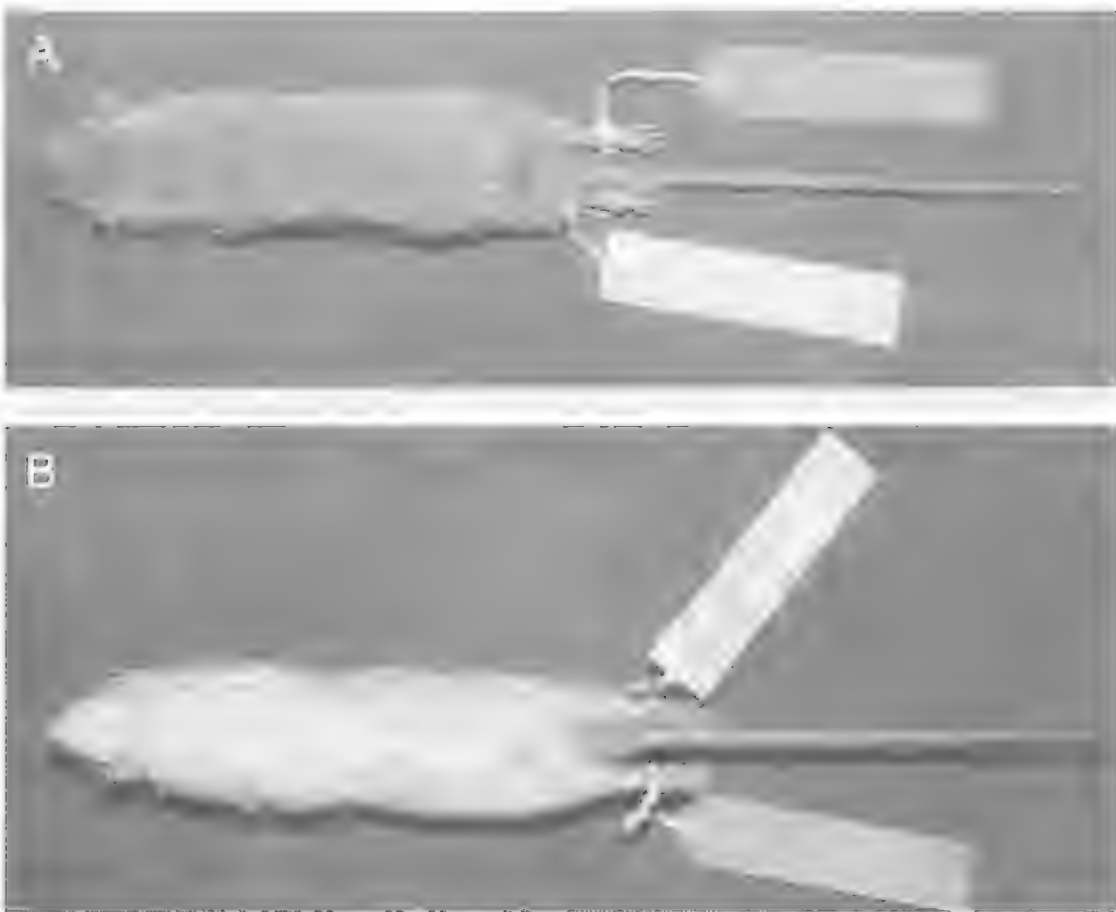


FIG. 40. Holotype of *Antechinus wilhelmina* Tate, 1947 (now *Murexechinus melanurus*). AMNH 109811, study skin; A, dorsal view; B, ventral view. TL = 238mm; HB = 108mm; TV = 130mm; HF = 20mm.

In light of the mixture of Tate's descriptive features for *habbema* and Laurie's new species (*hageni*) it is strange that the name *wilhelmina* should have persisted as the third species of New Guinean 'antechinus' (with *naso* and *melanurus*) to the present day e.g., Laurie & Hill (1954), Ziegler (1977), Ziegler (1982), Kirsch & Calaby (1977), Corbet & Hill (1980), Honacki et al. (1982), Baverstock et al. (1990). Archer (1982a), preferred to refer to the specimens of *wilhelmina* by collection locality (Mt Wilhelm) and museum accession number. Jenkins & Knutson (1983) assigned the *hageni* holotype to *wilhelmina*, while Westerman & Woolley (1993), Woolley (1994), Krajewski et al. (1996) and Armstrong et al. (1998) recognised *wilhelmina* and *habbema* as specifically distinct.

DISTRIBUTION (Fig. 42). From sea level to mid-montane areas of the central cordillera (up to

2,800m). Between 134°00'E in W Irian Jaya to 151°01'E (Normanby Island). It has been collected in rainforest, mid-montane forest, beech forest, pandanus forest and mossy forest. Full floristic details of collection localities appear in Archbold et al. (1942: 258), Brass (1964: 109) and Brass (1959: 41, where the largest recorded specimen was collected [and referred to as *longicaudata*]). Menzies (1972) recorded 2 maxillary fragments of *melanurus* from sparsely wooded *Eucalyptus* savannah near Port Moresby.

REPRODUCTION. All pouches examined had 4 teats. Lactating females were collected in (dates included in parentheses), January (1), August (17,22,26), September (12, 19), October (13, 20), November (10), December (16). Dwyer (1977) noted the capture of lactating females in April (7, 17), September (13, 21) and December (8).



FIG. 41. Holotype of *Antechinus wilhelmina* Tate, 1947. AMNH109811, cranium and dentary. Sex – m; BL = 26.64; ZW = 16.90; IO = 6.91; OBW = 10.61; IBW = 4.79; R-LC¹ = 5.29; R-LM¹ = 9.47; R-LM² = 11.75; R-LM³ = 14.00; R-LM¹T = 7.48; M²W = 1.75; I¹-M¹ = 14.76; P¹⁻¹ = 3.72; M¹⁻⁴ = 6.33; Dent = 21.44; I₁-M₄ = 12.72; P₁₋₃ = 3.44; M₁₋₄ = 6.67; M₂W = 1.18.

DESCRIPTION. *Mean Measurements.* External (mm): total length (head, body, tail) (♂) 256, (♀) 230; tail (to cloaca) (♂) 135, (♀) 130; hind foot (su) (♂) 22.55, (♀) 21.44; ear (notch) (♂) 15.92, (♀) 15.65. Skull: basicranial length (♂) 27.30, (♀) 25.99; M¹⁻⁴ length (♂) 6.81, (♀) 6.72; M¹⁻⁴ width (♂) 1.90 (♀) 1.89. (Table 6).

P₄ Morphology. P¹ may be single, or double-rooted (of 9 pairs of P⁴ examined, 4 pairs were

single-rooted, 5 pairs double-rooted) but all crowns were molariform, the most significant cusp being the metacone. Other features include a small cusp homologous to a paracone. P₄ was always single-rooted as either a peg-like spur, or premolariform and relatively bulky. When heavily built, this tooth was often oriented obliquely in the dentary.

SIZE. In *M. melanurus* body size decreases significantly with increasing altitude. Using basiscranial length BL as a reflector of overall body size, its average value in adult specimens of both sexes collected lower than 1,000m a.s.l. mean=32.52mm (R=29.29-36.83, N=6, SD=2.50), at altitudes greater than 1,000m a.s.l. but less than or equal to 2,000m a.s.l. BL mean=26.85mm (R=23.11-30.33, N=23, SD=1.86), and at altitudes greater than 2,000m a.s.l. but less than or equal to 3,000m a.s.l. BL mean=25.75mm (R=22.23-28.33, N=12, SD=1.74).

The pattern is similar for males and females if treated separately. The largest individual examined was ♂ AMNH 159473 (BL=36.83mm) from Mt Pabinama, Normanby Island (10°06'S 151°01'E) at 820m.

The smallest adult examined was ♀ AMNH 109815 (BL=22.23mm) from 9km NE Lake Habbema (04°05'S, 138°50'E) at 2,200m. Largest specimens have come from the NW-SF extremities of the island.

COLOUR (Fig. 43). The intensity of fur colour in *M. melanurus* is highly variable, and individuals of all colour forms, from drab to brilliant can be found from sea level through to 2,500m a.s.l. A significant trend of colour enhancement occurs, however, from the north west through to the south eastern tip of the island. All study skins examined were assigned a subjective colour rating (C), 1 (for extremely drab) through to 5 (for very brightly coloured individuals with rich tones). The trend can be further demonstrated by dividing the island into longitudinal blocks. For specimens collected west of longitude 140°00'E the average colour rating $C=2.03$ (R=1.0-3.5, N=19, SD=0.90), for specimens collected between 140°01'E and 146°00'E $C=2.98$ (R=2.01-4.0, N=24, SD=0.73), and for those between 146°01'E and 150°00'E $C=3.7$ (R=2.0-5.0, N=21, SD=0.73).

SPECIMENS EXAMINED. Araboe-biyak, 1750m, 03°51'S 136°26'E (RMNH 1839, RMNH 1936); Aruu, Krake Mts, 1400m, 06°20'S 146°05'E (AMNH 190868); Arafak Mts, 1000m, 01°09'S 134°00'E (BMNH 2952757); Aroa River, 09°05'S 146°48'E (BMNH 1939.3239); Baiyanka, 2287m, 05°35'S 144°51'E (BMNH 50.1100); Baiyanka, 2440m, 05°35'S 144°51'E (BMNH 50.1101); Bernhard Camp 4km SW, 850m, 03°30'S 139°12'E (AMNH 152034); Bialoi, Morobe, 686m, (MCZ 29337); Bonenu, 1220m, 09°54'S 149°25'E (BMNH 50.1106); Boohiari Mt (base), (FN 80); Bulolo 10km W, 780m, 07°11'S 146°39'E (BBM 51268, BMNH 54045); Collin's Sawmill, Mt Otu, 2660m, 05°59'S 145°25'E (AMNH 190866); Dayimbu Lake, 25m, 07°36'S 141°17'E (AMNH 105795); Dayman

Mt, 1540m, 09°49'S 149°16'E (AMNH 157075); Derimapa Mt, 1220m, 03°50'S 135°43'E (AMNH 101978, BMNH 33.6168); Derimapa Mt, 1525m, 03°50'S 135°43'E (BMNH 33.6169); Enaena, 1220m 10°03'S 149°38'E (BMNH 50.1102); Enaena, 1372m, 10°03'S 149°38'E (BMNH 50.1104-50.1105); Enaena, 1525m, 10°03'S 149°38'E (BMNH 150.1103); Erimbai Mt, 2500m 06°12'S 145°20'E (QM JM 1093-1094); Fermain, 1372m, 05°14'S 141°40'E (BBM 22905); Fly River, 80m, 05°20'S 147°57'E (AMNH 105027); Galawe Mt, 2100-2140m, 06°03'S 143°53'E (BMNH 53.202-53.203); Galawe Mt, W slopes, 2684m, 06°03'S 143°53'E (CM 14); Givariu River, 200m, 09°40'S 149°17'E (AMNH 157075); Habbema Lake 18km N, 2200m, 04°05'S 138°42'E (AMNH 157075, AMNH 109794, AMNH 109805, AMNH 109828, AMNH 150988, AMNH 109821); Habbema Lake 9km NE, 2200m, 04°05'S 138°50'E (AMNH 109815, AMNH 109811, AMNH 109819); Hagen Govt, Sin 25km N, 1525m, 05°49'S 144°07'E (BMNH 50.1839); Hagen Mt., 2134-2440m, 05°54'S 144°09'E (AMNH 156357, AMNH 156362-156363, AMNH 156365-156366); Hagen Mt., 2135-2440m, 05°54'S 144°09'E (AMNH 156371, AMNH 156379, AMNH 156381-156387, AMNH 156390, AMNH 156401); Hagen Mt., 2501m, 05°54'S 144°09'E (AMNH 156356); Hagen Mt., 2592m, 05°54'S 144°09'E (AMNH 156358, AMNH 156360, AMNH 156369, AMNH 156377); Idenberg R., 50m, 03°31'S 139°11'E (AMNH 152026); Idenberg R., 1200m, 03°31'S 139°11'E (AMNH 152032); Idenberg R., 03°31'S 139°12'E (AMNH 152033); Iuki, 350m, 10°35'S 150°00'E (AMNH 108559); Java Route, 20km E Sogeri, 600m, 09°25'S 147°26'E (BBM 60270); Krake Mts, 1350m, 06°13'S 146°01'E (AMNH 190871); Krake Mts Aruu, 1400m, 06°20'S 146°05'E (AMNH 190869); Krake Mts Aruu, 06°20'S 146°05'E (AMNH 190870); Madang, Aitua, 1159m, 04°48'S 145°20'E (AMNH 198721); Madulu, 1255m, 08°31'S 147°00'E (AMNH 104051); Matsika, 980m, 08°35'S 146°54'E (AMNH 104052); Minj, 1830m, 05°50'S 144°39'E (BMNH 53.199); Misim Mt., 1738m, 07°13'S 146°50'E (MCZ 29920); Mola-Kokoda Road, 900m (AMNH 108562); Moreka, 1300m, 09°24'S 147°32'E (MCSNCE 3915); Mur Mur Pass, 2700m, 05°45'S 145°56'E (BBM 97458); Mur Mur Pass, 2800m, 05°45'S 143°56'E (BBM 60674); Nondugl, 1900m, 05°52'S 144°45'E (AMNH 183817); Oksapmin, 1800m, 05°15'S 142°14' (BMNH 99905); Oksapmin, 1900m, 05°12'S 141°38'E (BBM 55431); Orarebari, 3m, 01°21'S 134°18'E (AMNH 221628); Otu Mt., 2200m, 05°59'S 145°25'E (AMNH 190867); Pabinama Mt, Normanby I., 280m, 10°06'S 151°01'E (AMNH 159473); Schrader Mts, 2440m, 05°10'S 144°26'E (BMNH 69297); Shungol Mt., 2000m, 06°51'S 146°44'E (BBM 98282); Sibil Valley, 1250m, 05°00'S 141°00'E (BBM 222, RMNH 16932); Stuart I. (opposite), (AMNH 105854); Tambul 10km NNE, 2700m, 05°45'S 143°56'E (BBM 97406); Telefomin, 1525m, 05°12'S 141°38'E (BBM 99733, JM 6170, JM 6171); The Gebroeders, 1525m, 03°50'S 135°43'S (BMNH 1939.3238); Tomba Mt., 2501m, 05°50'S 144°02'E (BMNH 50.1836); Tomba Mt., 2592m, 05°50'S 144°02'E (BMNH 50.1834-50.1835); Tomba Mt., 05°50'S 144°02'E (M 9560); Utakwa River, 1661m, 04°11'S 137°37'E (BMNH 156369); Wamman 4km N, 1200m,

04°48'S 146°19'E (BBM 103798); Welya, 2592m, 05°44'S 143°56'E (BMNH 53200); Wilhelm Mt., 2500-2370m, 05°46'S 144°59'E (AMNH 190895); Wilhelm Mt. E slopes, 2770m, 05°46'S 05°46'S 144°59'E (AMNH 190865).

PHYLOGENETICS

CHARACTER ANALYSIS. Although Nixon & Carpenter (1993) assert that one does not need to know 'primitive' and 'derived' states before attempting analysis, I have included here a short evaluation of the determination of polarity of characters used to assess relationships among 'antechinuses' and 'murexias'. Although phylogenies of identical topology will naturally be produced from analyses with reversed polarity (i.e., without prior appreciation of polarity) the weight of palaeontological evidence suggesting overall trends of derivation in dasyuroids and didelphoids makes analysis of phylogenies based on reversed polarities untenable (i.e., defending such character transformations as possession of P₃, widely spaced premolars, upper incisor number 8, large 3-cusped M₄ talonid etc, as derived conditions).

The decisions of polarity expressed in the matrix that follows have relied heavily on the discussions of Archer (1976b, 1981, 1982a, 1982b), Kirsch & Archer (1982) and Reig et al. (1987) and their interpretation of the fossil record.

Incisors. Incisors are commonly absent in the fossil record, however, Archer (1976b) considered the following conditions of upper incisor morphology to be plesiomorphic in dasyurids: V- or U-shaped upper incisor rows (Character 1); I¹ and I² separated by a small diastema (Ch. 7); hypsodont condition of I¹ relative to I² correlated to a diastema between I¹ and I² and crowns non-spatulate (Chs 8, 9); I⁴ longer-crowned than I³ (Chs 11, 15) (Archer found this condition clouded in *Antechinus* because the then broader interpretation of the genus included New Guinea taxa). While in the present analysis variation in crown size in lower incisors did not provide a usable transformation series, the relative size of the lingual incisor heel did. I could find no prior polarity assessment of this feature, and on the basis of the upper incisor trends noted above, have treated a greatly reduced lower incisor heel as derived (Ch. 39). Peg-like morphology in upper and lower incisors has also been postulated as the plesiomorphic condition for didelphoids, any increased spatulation or reduction/enlargement in size representing a derivation (Reig et al., 1987). The polarity assigned to

characters 3, 4, 6, 8, 10, 12, 13 and 15 is an extension of this opinion and incorporates similar polarity decisions made by Kirsch & Archer (1982) for characters 4, 8, 9, 11 and 14 in particular. Procumbency of upper incisors (Ch. 2) and prostration of lowers (Ch. 38) are regarded here as derived features, decisions based on comments on specialisation by Archer (1976b) and the condition in the majority of didelphoids (Reig et al., 1987).

Canines. Caniniform canines are regarded to represent the primitive state in didelphoids and dasyuroids (Archer, 1976b, 1981). Characters 16, 17, 18, 19 and 20 are polarised accordingly, and incorporate putative derived conditions of root/crown definition and presence of a posterior cusp on C¹ from comparison with the didelphoid record (Reig et al., 1987).

Premolars. Archer (1976b) proposed that narrow premolars in uncrowded premolar rows represent the primitive premolar condition in didelphoids and hence dasyuroids (Chs 21, 22, 23, 43, 48). He noted a direct correlation between the development of shorter and wider premolars with extreme shortening of the premolar row (Ch. 25). Elsewhere he noted (Archer, 1981) that reduction of P₃, widening of the premolars and crowding of the premolar tooth row are derived states within the genus *Sminthopsis* as well as within dasyurids as a whole. Tate (1947) noted short muzzles and short palates accompanying short, crowded tooth rows in more derived vertebrate-killing dasyurids. Reig et al. (1987: 12) concluded that the primitive condition in didelphoids for upper premolars was one of 'well-developed, trenchant, narrow teeth increasing in size from the first to the third' (Chs 40, 41, 42, 44, 45, 47). They also considered bulbousness in P₃ a derived condition. Given the absence of lingual and buccal cingula from ancestral forms, cingulation of lower premolars (Ch. 46) was assumed to represent the derived condition. The presence/absence of a posterior cusp on P₃ (Ch. 24) was a condition for which there was little comment in recent literature, and one which exhibited great variability within the didelphoids. Given that the development of a strong posterior cusp on P₃ appeared to be associated with an increase of buccal cingulation, I have treated pronounced cusping of P₃ as derived, but concede that this decision may be ill-advised.

Molars. Archer (1976b) and Wroe (1999) noted that the anterior cingulum of upper molars was complete in ancestral didelphids and is regarded

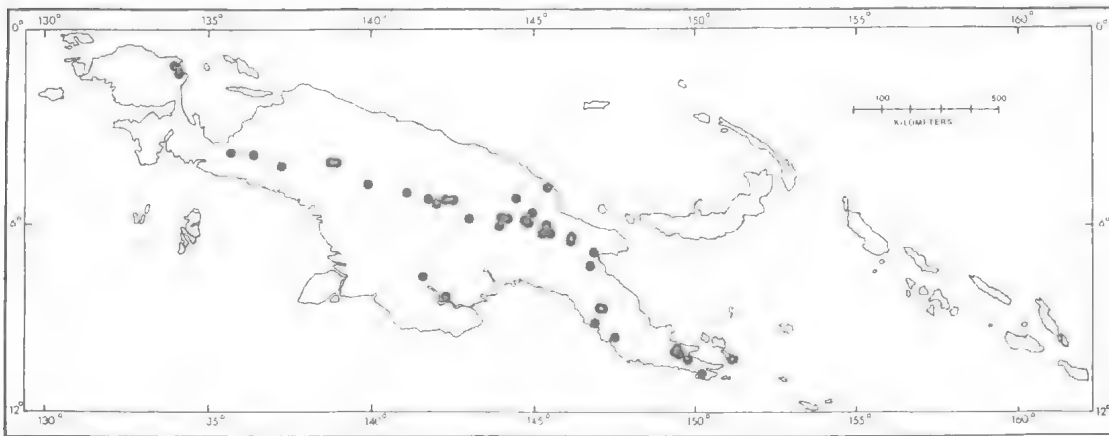


FIG. 42. Distribution of *Murexeichinus melanurus*.

as representing the primitive state in dasyuroids (Ch. 26). Cingulum width is inversely related to the width of molars according to Archer. Reig et al. (1987) added that a bulbous, non-compressed protocone on the upper molars (Chs 27, 31) was representative of the primitive condition along with the length of M^2 being longer or subequal in length to M^3 (Ch. 28). Support for regarding the presence of stylar cusp B as plesiomorphic and its reduction or loss as apomorphic is presented by Archer (1976b) and Muirhead & Archer (1990). The close proximity of the paracone to stylar cusp B (Ch. 37) is regarded as an apomorphic condition (Kirsch & Archer, 1982). Archer (1976b) did not use the condition of stylar cusp D in his analysis given that stylar cusp pattern did not appear to distinguish between genera. Reig et al. (1987: 11) addressed the ancestral condition of stylar cusp D thus 'the anatomy of the molar teeth in Lower Cretaceous therians and in *Alphadon* and *Peradectes* indicates that a well-developed stylar shelf with a complete series of stylar cusps ['stylar shelf with usually five regular-sized stylar cusps' p.13], but without enlargement of the metastylar area is the primitive condition' (Ch. 33). Well-developed ectoflexus in the ectoloph of upper molars (Ch. 34) is considered apomorphic for dasyurids (Muirhead & Archer, 1990), as is reduction or loss of the M^4 metacone (Ch. 35) (Archer, 1976b), loss of upper molar posterior cingulum (Ch. 36) and reduction or loss of M_1 paraconid (Chs 49, 53) (Kirsch & Archer, 1982). Tall, well-developed entoconids are regarded as an ancestral condition and are known from all Cretaceous didelphids (Archer, 1976b; Kirsch & Archer, 1982; Muirhead & Archer, 1990;

Muirhead, 1994; Wroe, 1999). Archer (1981) commented concerning entoconids in dasyurids, that species occupying higher rainfall areas such as those of highland New Guinea had well developed entoconids while many Australian arid-adapted dasyurids lack them, and that the absence of entoconids in Australian dasyurids is a derived condition. Any reduction of M_4 talonid cusps below 3 (Ch. 51) is regarded as a derivation as well as reduction of the M_3 talonid width (Ch. 50) (Archer, 1976b; Kirsch & Archer, 1982). Transverse metacristids (Ch. 54) are considered structurally primitive (Archer, 1976b) among dasyurids and the condition is thought to reflect a more insectivorous diet. The orientation of the M^4 preparacrista (Ch. 32) is here assumed to be in the primitive condition when it is transverse to the long axis of the skull. This notion receives support from examination of the condition in a number of microbiotheroids and didelphoids (*Dromiciops*, *Pedimys*, *Glironia*, *Caluromys*, *Philander*, *Metachirus*, *Micoures*, *Marmosa*, *Monodelphis*, *Thylatheridium*, *Lutreolina*, *Thylophorops*, *Sparassocynus*, *Didelphis*, *Chironectes*). Orientation in highly derived dasyurids (e.g. *Sarcophilus*, *Thylacinus*) is more oblique, maximising the shearing capacity of the M_4 postprotocristid.

A picture of relative rostral width (and, ultimately an index of brachycephaly) (Ch. 55) is given by comparing skull width across the lachrymal canals against rostral length measured from I^1 to the lachrymal canal. In the suite of taxa I have reviewed for this study, values varied from approximately 67% (in *Thylacinus*) to approximately 104% (in *Sarcophilus*). While the primitiveness of *Thylacinus* is debatable, I have

assumed that because short muzzles are a direct result of shortened check-tooth rows, that brachycephalic skulls can be regarded as representing the derived condition. Archer (1981) interpreted brachycephaly as a derived condition. The convexity or fluting of nasals (Ch. 56) was considered a primitive condition after examining the range of variation in a number of didelphoids for which specimens or figures (e.g., Reig et al., 1987) were available (*Dromiciops*, *Caluromys*, *Philander*, *Metachirus*, *Marmosa*, *Monodelphis*, *Lestodelphys*, *Lutreolina*, *Didelphis*, *Chironectes*). Expansion of the tympanic wing of the alisphenoid (Ch. 57), and that of the pars mastoidea (Ch. 58) are both considered derived states (Kirsch & Archer, 1982) as are squamosal-frontal contact (Ch. 61) and possession of palatine vacuities (Ch. 62) (Archer, 1981). (Given the division of opinion regarding the assignment of polarity to the condition of maxillary vacuities (Marshall, 1977 vs Archer, 1982b vs Reig et al., 1987) I opted not to use this character in the data analysis).

While Archer (1981) regarded narrow nasals (Ch. 59) in *Sminthopsis* to represent a derived condition, I have broadened the concept of 'narrowness' to include gentle flaring posteriorly inasmuch as the boundary of the nasal remains reasonably straight along its longitudinal length. This state represents the nasal condition in the majority of didelphoids. Greater posterior expansion of the nasals I have regarded as derived. 'Doming' of the skull (Ch. 60) also is interpreted differently to Archer's (1981) concept of it, where he sought to describe the swelling of the nasal-frontal sutures ('Roman-nosing') in *Sminthopsis virginiae* and *S. douglasi*. Here, I am attempting to distinguish between the gentle flex in the antero-posterior profile of the skull seen in didelphoids and the extreme dolichocephalic condition found in *Planigale*. Accordingly I have regarded the 'gentle dome' as the plesiomorphic condition and extreme dorso-ventral flattening as derived. The morphology of the supratragus (Ch. 63) has been useful in distinguishing species of *Antechinus* (Van Dyck, 1980), however assigning correct polarity to the various states of the supratragus is subjective. Here I regard the more simple paddle-like condition as plesiomorphic, while the more florid, twisted and corpulent structures I have treated as derived. Tail length (Ch. 64) is also polarised subjectively, but guided by Archer's (1981) decision that long tails probably represent a derived condition. I have extended

this to include very short tails. The decision on tail length polarity, however, was ultimately based on the condition found in living microbiotheriids such as *Dromiciops* which is similar, dentally and cranially, to Late Oligocene-Early Miocene *Microbiotherium* (Marshall, 1982; Segall, 1969 cited in Reig et al., 1987). I have therefore regarded a tail length of slightly less than head-body length as representative of the primitive condition.

The development of striated calcaneal pads (Ch. 65) is an extraordinary development confined to two New Guinea taxa. I have treated this condition as derived as also I have the condition of extremely long claws (Ch. 66) (seen in *Antechinus swainsonii* and *A. minimus*), longitudinal body stripes (Ch. 67) and brushed tails (Ch. 69). These subjectively polarised derivations are very rare within the study group and amount more to autapomorphies useful in describing the taxa in which they occur.

I have assigned polarities to pouch condition (Ch. 68) after the argument of Reig et al. (1987) who concluded that the presence of a pouch was the derived condition, and that pouch evolution occurred repeatedly within Didelphoidea. Small body size is regarded as the plesiomorphic condition (Ch. 70).

Penile morphology is difficult to polarise with confidence. Reig et al. (1987: 38) conclude on the basis of commonality and outgroup comparison with reptiles, monotremes and placentals that 'the bifid glans is thus considered the plesiomorphic condition in didelphimorphs and in marsupials as a whole'. Woolley (1987), however, concluded that the simple, non-bifid penises of *Dasyuroides byrnei*, *Dasyercus cristicauda* and *Dasykaluta rosamondae* suggested primitive anatomy. Reig et al. (1987: 38) cite Barbour (1977: 241) in suggesting that in *Didelphis marsupialis*, *Philander opossum*, *Marmosa mexicana* and *Caluromys derbianus* '... as in all other marsupials except the macropodids, *Tarsipes* and *Notoryctes*, the glans penis is cleft, bifid and divided ...', but much earlier, Woolley & Webb (1977: 309) had noted 'in others [marsupials] the tip is undivided, and either tapered or blunt' and later Woolley (1982) demonstrated non-bifid penis anatomy and accessory structures in a suite of species (*D. rosamondae*, *Pseudantechinus macdonnellensis*, *P. ningbing*, *Parantechinus bilarni* and *P. apicalis*). In looking for the plesiomorphic dasyurid condition I have (rightly or wrongly)

TABLE 6. Absolute measurements for *Murexechinus melanurus*. See 'Methods' for limits of measured dimensions and Table 1 (caption) for abbreviations.

Measurement		N	mean±r	OR	SD	V	CV
BL	M	41	27.30±0.43	22.93-36.83	2.72	7.38	9.96
	F	22	25.99±0.41	22.23-30.12	1.94	3.77	7.46
	T	64	26.83±0.32	22.23-36.83	2.53	6.41	9.43
ZW	M	42	17.16±0.25	14.58-21.83	1.61	2.58	9.38
	F	20	16.34±0.31	13.81-18.55	1.37	1.86	8.38
	T	63	16.89±0.20	13.81-21.83	1.57	2.46	9.30
IOW	M	43	7.09±0.04	6.51-8.14	0.28	0.08	3.95
	F	21	7.06±0.07	6.50-7.67	0.32	0.10	4.53
	T	65	7.09±0.04	6.50-8.14	0.30	0.09	4.23
OBW	M	40	11.05±0.11	10.26-13.73	0.71	0.50	6.43
	F	19	10.86±0.16	9.92-12.02	0.69	0.48	6.35
	T	60	10.99±0.09	9.92-13.73	0.70	0.49	6.37
IBW	M	41	5.11±0.10	4.23-7.15	0.63	0.39	12.33
	F	19	5.13±0.14	4.30-6.25	0.60	0.36	11.70
	T	61	5.12±0.08	4.23-7.15	0.61	0.38	11.91
R-LC ¹	M	43	5.53±0.09	4.93-7.80	0.60	0.36	10.85
	F	22	5.24±0.11	4.40-6.28	0.53	0.29	10.10
	T	66	5.43±0.07	4.40-7.80	0.59	0.35	10.87
R-LM ¹	M	43	9.80±0.11	8.97-12.69	0.73	0.53	7.45
	F	22	9.53±0.19	8.35-11.17	0.87	0.75	9.13
	T	66	9.71±0.10	8.35-12.69	0.78	0.61	8.03
R-LM ²	M	34	11.96±0.16	10.78-15.62	0.96	0.91	8.03
	F	16	11.83±0.26	10.09-13.66	1.05	1.10	8.88
	T	51	11.91±0.14	10.09-15.62	0.98	0.96	8.23
R-LM ³	M	39	14.26±0.11	12.73-18.50	1.20	1.44	8.42
	F	18	13.87±0.24	12.03-15.78	1.03	1.05	7.43
	T	58	14.12±0.15	12.03-18.50	1.16	1.34	8.22
R-LM ¹ T	M	42	7.72±0.10	6.97-10.42	0.68	0.47	8.81
	F	19	7.65±0.12	6.83-8.85	0.54	0.29	7.06
	T	62	7.69±0.08	6.83-10.42	0.64	0.41	8.32
I ¹ -M ⁴	M	43	15.06±0.20	13.85-20.04	1.32	1.74	8.76
	F	22	14.55±0.23	13.17-16.81	1.10	1.20	7.56
	T	66	14.88±0.16	13.17-20.04	1.26	1.60	8.47
P ¹⁻³	M	43	3.39±0.05	2.95-4.70	0.33	0.11	9.73
	F	22	3.34±0.08	2.90-4.09	0.37	0.13	11.08
	T	66	3.37±0.04	2.90-4.70	0.34	0.12	10.09
M ¹⁻⁴	M	43	6.81±0.08	6.29-8.67	0.51	0.26	7.49
	F	22	6.72±0.09	6.20-7.49	0.40	0.16	5.95
	T	66	6.78±0.06	6.20-8.67	0.47	0.22	6.93
M ² W	M	44	1.90±0.06	1.75-2.41	0.41	0.02	21.58
	F	22	1.89±0.03	1.70-2.15	0.15	0.02	7.94
	T	67	1.89±0.02	1.70-2.41	0.15	0.02	7.94
Dent	M	44	21.63±0.32	18.55-29.40	2.11	4.45	9.75
	F	22	20.69±0.36	17.55-24.53	1.69	2.86	8.17
	T	66	21.31±0.25	17.55-29.40	2.01	4.05	9.43
I ₁ -M ₄	M	44	13.14±0.17	12.10-17.62	1.15	1.33	8.75
	F	21	12.62±0.19	11.41-14.38	0.85	0.71	6.74
	T	66	12.96±0.13	11.41-17.62	1.09	1.18	8.41
P ₁₋₃	M	44	3.47±0.06	2.97-4.80	0.37	0.14	10.66
	F	22	3.41±0.06	3.00-4.08	0.30	0.09	8.80
	T	67	3.45±0.04	2.97-4.80	0.35	0.12	10.14
M ₁₋₄	M	44	7.42±0.09	6.67-9.65	0.63	0.39	8.49
	F	22	7.30±0.12	6.50-8.40	0.54	0.29	7.40
	T	67	7.37±0.07	6.50-9.65	0.60	0.01	8.14
M ₂ W	M	44	1.23±0.02	1.07-1.61	0.11	0.01	8.94
	F	22	1.20±0.02	1.05-1.37	0.09	0.01	7.50
	T	67	1.22±0.01	1.05-1.61	0.10	0.01	8.20
TL	M	16	256±8.50	192-330	34	1171	13.28
	F	9	230±4.67	205-248	14	209	6.09
	T	25	247±6.20	192-330	31	981	12.55
T	M	31	135±2.87	101-165	16	271	11.85
	F	18	130±2.36	110-143	10	106	7.69
	T	49	133±2.00	101-165	14	216	10.53
HF	M	30	22.55±0.47	16-31	2.55	6.49	11.31
	F	18	21.44±0.34	19-23.5	1.46	2.14	6.81
	T	48	22.27±0.31	19-31	2.12	4.48	9.52
E	M	25	15.92±0.20	15-18	1.01	1.01	6.34
	F	13	15.65±0.27	14-18	0.97	0.97	6.20
	T	38	15.83±0.16	14-18	1.00	1.00	6.32

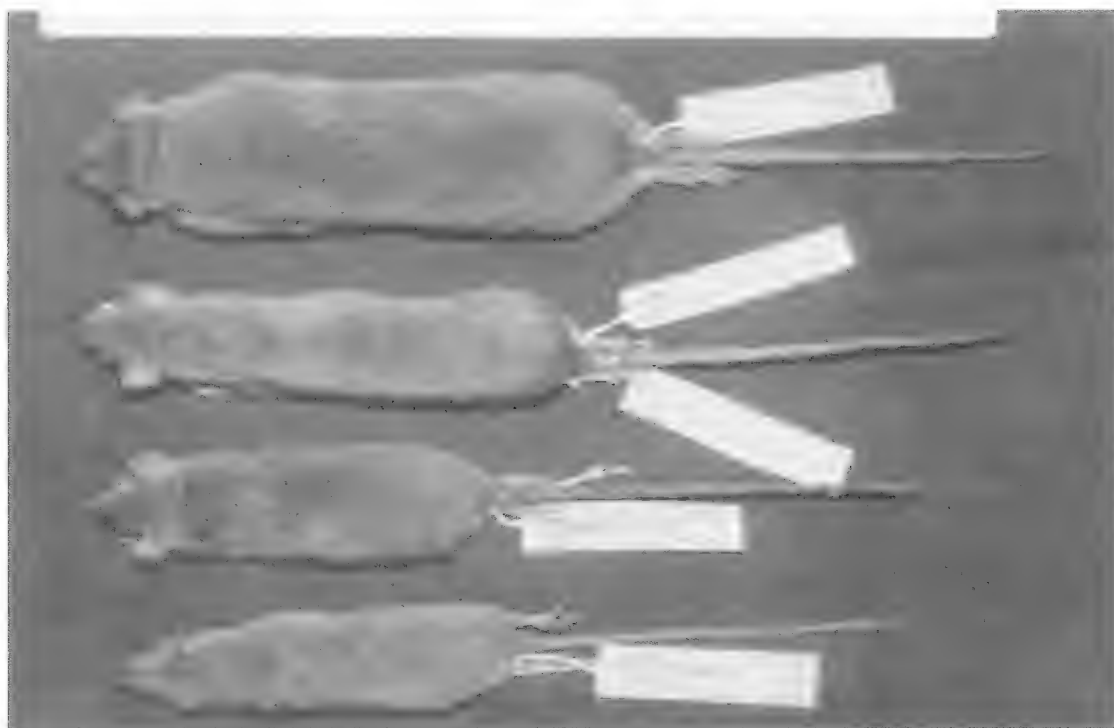


FIG. 43. Size and colour variation in *Murexechinus melanurus*. From the top AMNH 159473 Mt Pabinama, Normanby I. (m); AMNH 221628 Geelvink Bay, Oransbari (m); AMNH 108559 Itiki (m), AMNH 109828 Bele R. 18km N Lake Habbema (f).

assigned the simplest condition (the urethra terminating at the end of a simple non-bifid glans as in *D. rosamondae*) as the plesiomorphic condition; other forms of the penis (bifid glans, deeply cleft and divided penis, acquisition of corpora cavernosa and/or a penile appendage) are considered derivations.

Semelparity (Ch. 72) is treated here as a derived condition (Strategy 1 of Lee et al., 1982) on the arguments of Braithwaite (1973) and Lee & Cockburn (1985). Polarity assignment to nipple number (Ch. 73) can only be made subjectively, but for dasyurids, the plesiomorphic nipple number should correlate with the plesiomorphic reproductive strategy and not that of Strategy 1 species (monoestrous or facultative monoestrous taxa confined to predictable, highly seasonal geographic regions and dominated by 'pouches' with high nipple numbers). This is a departure from the argument of Reig et al. (1987) who consider that for didelphoids (which are polyoestrous, polytocous and seasonal breeders (Lee & Cockburn, 1985) frequently sporting a high and variable number of nipples (4-27) in

both abdominal and inguinal concentrations), fewer than nine nipples represents the derived state. Instead I would suggest that for primitive dasyurids lower nipple number represented by the Strategy IV-VI species (polyoestrous, breeding all year round) most closely expresses the primitive condition. This decision is also partly influenced by the nipple condition found in *Dromiciops*, which is four (Mann, 1958 cited in Reig et al., 1987).

PHYLOGENETIC ANALYSIS. The distribution of character states used to help resolve the affinities of *Antechinus* and *Murexia* is presented in Table 7. The first 37 characters relate to the upper dentition (15 features of the upper incisors, 5 of the upper canines, 5 of the upper premolars) while the following 17 relate to the lower dentition (2 for lower incisors, 9 for lower premolars, 6 for lower molars). Eight cranial characters were scored along with 11 external features. Character 73 relates to post-mating mortality in males. The transition series is not completely comprehensive and includes some characters whose polarities have

been determined by subjective criteria, but at the least, the characters used are compatible with earlier studies thereby enabling comparison of the results of analysis.

The phylogenetic analysis associated with this study was aimed primarily at resolving the affinities of the New Guinea taxa with Australian *Antechinus*. The distribution of character states for 73 characters (Table 7) among 33 taxa (with the addition of a hypothetical ancestor) is listed in Table 8. The analyses were run with characters unweighted and unordered (although successive weighting and ordered runs produced basically the same results). Ordered (unweighted) analysis produced one most parsimonious tree. Unordered (unweighted) analysis produced 15 trees of length 511, Consistency Index (Kluge & Farris, 1969) 0.46, and Retention Index (Farris, 1989) 0.69. The analysis was repeated using PAUP with 10 random addition sequences with identical results. The strict consensus of the most parsimonious trees (Fig. 44) shows (among other things) that the relationships between *M. habbema*, *M. longicaudata* and *P. naso* cannot be satisfactorily resolved. Synapomorphic character changes defining major clades are as follows: Dasyuridae, node 54: 8 (0>1), 14 (0>1), 31 (0>1), 46 (0>1), 51 (0>1); 54 (0>1); Australian taxa, node 51: 26 (0>1), 27 (0>1), 30 (0>1), 37 (0>1), 56 (2>3); the Planigalidae, node 50: 60 (2>3), 68 (1>2), 73 (3>4); the Phascogalidae, node 42: 71 (0>1); *Phascogale* node 34: 8 (4>5), 11 (3>4); the Dasyurinae, node 47: 53 (0>1); the Sminthopsinae, node 49: 26 (1>2), 62 (0>1).

The *Antechinus* clade of Fig. 44 is defined, at node 42, by Character 71 (penis with a bifid tip); node 40 (the *A. swainsonii*-*A. minimus* clade) by Character 66 (claws very long); node 39 is defined by Characters 17 (C^1 root and crown clearly differentiated) and 73 (nipple number high and variable). Nodes 41, 36 and 38 are not defined by synapomorphies but described by a series of homoplasious forward changes. Node 37 is described by Character 8 (I^{2-4} crowns broader than roots), and node 35, the root of the *A. adustus*, *Phascogale* clade, is defined by 4 synapomorphies, Characters 2 (markedly procumbent incisors, 3 (I^1 crown much heavier than root), 12 (I^{1-4} heavily cingulated) and 15 (I^2 greatly enlarged). *Phascogale* (node 34) is defined by synapomorphies of Characters 8 (I^{2-4} crowns much heavier than roots) and 11 ($I^2 > I^3 > I^4$).

The morphological comparisons presented here suggest that the New Guinea taxa *M.*

habbema, *M. longicaudata*, *P. naso*, *P. rothschildi* and *M. melanurus* represent a suite of related but morphologically primitive taxa that lack clear signs of close relationship to each other but which have minor autapomorphies to serve to distinguish them from one another. They are largely plesiomorphic in their teeth and skulls relative to Australian *Antechinus* and other dasyurid genera. *Micromurexia*, *Phascomurexia* and *Murexia* are the most plesiomorphic and recognised by their common possession of the following: a spur or peg-like I^1 with its crown extremely high; I^{2-4} with narrow crowns and unfolded cusps; $I^4 > I^3 > I^2$; long, fine, needle-like C^1 ; an uncrowded upper premolar row where P^3 does not possess a posterior cusp; broad upper molars with complete anterior cingula; M^1 whose anterior margin is convex or straight; broad protocone on M^{1-3} ; M^{1-2} with stylar cusp D a low crest; slight indentation on the M^{2-3} ectoloph; $I_{1,2}$ almost perpendicular; P_3 larger than, or slightly smaller than P_2 ; uncrushed premolar row and uncingulated P_3 ; well developed M_1 paraconid; M_4 talonid with 3 cusps; large entoconids; elongate rostrum with fluted nasals and domed skulls; poorly developed tympanic wings of the alisphenoid; simple penis morphology; rudimentary pouch and low nipple number (4).

Each, however possesses characters that might be considered more derived than the others. *M. habbema*, for example, has slightly cingulated I^{1-4} , upper premolars that are more rounded in occlusal view, $P_{1,2}$ that show postero-lingual lobing and a skull that is slightly less elongate. *M. longicaudata* has widely spaced upper first incisors, a more reduced M^4 protocone, heavier cingulation on P_3 , M_4 talonid on which the 3 cusps are much more reduced and hind foot pads more strongly and extensively developed. *P. naso* has markedly procumbent I^1 which is slightly more bulky and less needle-like than that seen in *M. habbema* and *M. longicaudata*. Its canines are shorter and thicker with root and crown becoming more differentiated, M^4 protocone is reduced as are the 3 cusps on M_4 , and it often has a white-tipped tail.

P. rothschildi is clearly more derived than either *M. habbema* or *P. naso* and shares no specially close relationship with *M. longicaudata*. Although possessing the following primitive features: M^1 very broad, with a wide protocone and complete anterior cingulum, the anterior margin of this tooth being straight or anteriorly convex, but not indented or concave; a slightly cingulated upper incisor row where

$I^2 < I^1 < I^4$; I^4 without a posterior cusp; M^1 and M^2 stylar cusp D a relatively low crest rather than a tall cone, skull elongate and domed; fluted nasals; poorly developed tympanic wing of the alisphenoid with contrasting expansion of the pars mastoidea and adjacent squamosal, the following represent derivations on that plesiomorphic frame: I^1 lightly built but curved (more claw-like) and slightly laterally compressed with heavier crown than *Micromurexia*, *Murexia* or *Phascomurexia*; I^1 and I^2 widely separated; upper canines long, thin (but bulkier and shorter than in *Micromurexia*, *Paramurexia* and *Murexia*), the root and crown being more differentiated than in any of those genera; an upper premolar row in which P^3 usually touches P^2 and M^1 ; P^1 and P^2 are rounded and show postero-lingual lobing; M^1 and M^2 stylar cusp B large (slightly smaller than stylar cusp D in M^1 , subequal in M^2); M^1 metacone reduced more than in *Micromurexia*, *Paramurexia* and *Murexia*; a lower premolar row in which the more rounded teeth are slightly crushed, and where P_3 is smaller than P_2 , cingulated P_3 ; paraconid on M_1 more reduced than in *Micromurexia*, *Paramurexia* and *Murexia*; three very poorly developed cusps on the M_3 talonid; entoconid of M_2 more reduced than in *Micromurexia*, *Paramurexia* and *Murexia*; long postmetatarsal pad and large heel pad on hind foot.

M. melanurus is the most derived member of the New Guinea taxa discussed here and it shares a closer relationship with Australian dasyurids than other New Guinea taxa. Superficially, *M. melanurus* is remarkably antechinus-like. Although, like other New Guinea taxa it possesses a very broad M_1 with a wide protocone and complete anterior cingulum with a straight or convex anterior margin, an I^4 without a posterior cusp, a relatively unreduced M^1 stylar cusp B, I_1 relatively perpendicular to the line of the dentary, an elongate and domed skull, poorly developed tympanic wing of the alisphenoid with expanded pars mastoidea and adjacent squamosal, the following represent major derivations seen commonly in the Dasyuridae: I^1 broad, claw-like and heavily crowned; I^{2-4} strongly cingulated buccally and lingually, blade-like and robust; $I^2 = I^3 = I^4$; C^1 short and thick; upper premolar row short, with premolars crowded, wide and robust; P^1 and P^2 in close contact; M^2 and M^3 with a more heavily indented ectoloph; lower premolars almost circular in occlusal view; lower molars

with weak entoconids and nasals flat rather than raised and fluted.

Externally, *M. melanurus* shares pelage colouration often found in Australian taxa, with rich rufous to light fawn post auricular patches and a definite change in colour from head to rump (usually agouti changing to warm russet) rather than uniform colour.

With respect to the Australian *Antechinus*, there is little doubt about the plesiomorphic nature of *A. godmani*, however my early contention (Van Dyck 1982a) that *A. godmani* was more closely related to New Guinea 'antechinuses' (in particular *A. mayeri* = *P. nasol*) than it was to Australian antechinuses, is clearly wrong, that opinion being based on a comparison of too few New Guinean specimens and an embarrassingly rich suite of symplesiomorphies. The impression of the primitiveness of *A. godmani*, however, remains, with its relatively poorly developed upper incisors with their broad roots and slight cingulation, the incisor 'gradient' $I^1 = I^2 = I^4$, needle-like upper canines, narrow uncrowded upper and lower premolar row, relatively low stylar cusp D of $M^{1,2}$, slight metacone of M^3 and less reduction in the M_3 talonid.

These features are highly refined in the sister pair *A. swainsonii* and *A. minimus*. While they retain those primitive features found in *A. godmani*, there is great specialisation of the upper incisors (I^1 being laterally compressed and spade-like with no diastema between I^1 and I^2 , I^{2-4} are lenticular), upper premolars (lensate, P^1 with pronounced cusp), upper molars (stylar cusp D of $M^{1,2}$ tall and conical), lower incisors (almost prostrate in *A. swainsonii*, slightly more erect in *A. minimus*) and lower premolars (widely spaced, lenticular). The tail is relatively shorter than in other antechinuses and the claws are longer. Given the high degree of derivation in these two species I favour the suggestion that *A. swainsonii* and *A. minimus* are sister species to *A. godmani*. (Having said that, I admit to a suspicion that we simply do not know with any real confidence whether the features seen in *A. swainsonii* and *A. minimus* are highly derived on an *A. godmani* frame, or the features seen in *A. godmani* are derivations on a primitive *A. swainsonii/A. minimus* frame.)

Antechinuses more derived than the *A. godmani/A. swainsonii/A. minimus* group display more typical dasyurid derivations such as a sharp incisor gradient ($I^2 > I^3 > I^4$); I^{1-4} heavily

cingulated; bulky, non needle-like C^1 with root and crown clearly differentiated and a small cusp present; a more rounded P^1 , a greatly reduced M^1 metacone; slightly crushed lower premolars; a broad P_3 and a less elongate skull.

The *A. flavipes* group (as per Baverstock et al. (1982)), consists of *A. leo* and *A. bellus* as sister species to *A. flavipes*. There has been little confusion with the identity of *bellus* in the past. Such features as its pale grey pelage, narrow interorbital width, broad zygomatics, broad rostral width, narrow upper incisors, relatively short canine, lack of posterior nasal expansion and expanded alisphenoid bullae have always served to make its identity clear. The identity of *leo*, however (in spite of its more club-shaped and widely separate L and RI^1 , relatively massive upper canines, very bulbous, crushed upper premolars and greatly reduced M^1 talonid), has long been masked by *flavipes* with which it has consistently been confused. Nonetheless, on the wider scale, the *bellus/leo* relationship is defined by very broad I^{2-4} crowns, and the two species share pronounced lingual lobing on $P^{1,2}$; a large posterior cusp on P^1 , absence of a posterior cingulum on M^x and simple supratragus of the ear.

A. adustus, *Phascogale tapoatafa* and *calura* share very procumbent, heavily crowned I^1 , heavily cingulated I^{1-4} and an enlarged I^2 , a suite of derived features which, along with a shared reproductive strategy (see Lee & Cockburn, 1985) supports the notion that phascogales might simply be highly derived antechinusines.

There is no doubt that the morphological comparison of New Guinea taxa presented in this study result in a phylogeny vastly different to those generated by recent genetic studies (e.g., Kirsch et al., 1990, Krajewski et al., 1993, Krajewski et al., 1994, Retief 1995, Krajewski et al., 1996, Krajewski et al., 1997, Armstrong et al., 1998). There is, however, some congruence between the morphology-based phylogeny of this work and that resulting from albumin immunology (Baverstock et al., 1990), particularly with respect to relationship between *Antechinus*, *Phascogale* and *Murexia*.

It is difficult to interpret these differences. The recommendation to reassign New Guinea 'antechinusines' to *Murexia* (Krajewski et al., 1996) was based on the resolution of the 'murexia' clade (*rothschildi*, *longicaudata*, *naso*, *melanurus*, *habbema*) achieved through analysis of cytochrome *b* sequences using *Planigale*

ingrami as its outgroup. The choice of *Planigale* as an outgroup might be criticised as inappropriate given its inclusion in the Dasyuridae. Morphology-based analysis selecting from Table 8 the same taxa as Krajewski et al. (1996) (*P. calura*, *P. tapoatafa*, *M. rothschildi*, *M. longicaudata*, *A. naso*, *A. melanurus*, *A. habbema*, *A. flavipes*, *A. swainsonii*, *A. stuartii*) and employing *Planigale* as the outgroup, results in a similar monophyletic New Guinea clade (*M. rothschildi*, *M. longicaudata*, *A. naso*, *A. melanurus*, *A. habbema*) but it is defined by 7 reversals (Characters 27, 29, 30, 37, 51, 60, 73), with 6 homoplasious reversals and 3 homoplasious forwards steps. (The node underpinning the Australian and New Guinean taxa is similarly defined by 14 reversals (Characters 11, 13, 31, 39, 40, 44, 48, 50, 51, 52, 55, 60, 68, 73) with 4 homoplasious reversals.

Armstrong et al. (1998) echoed the Krajewski et al. (1996) suggestion to reassign the New Guinea antechinusines to *Murexia* on the basis of their phylogeny of antechinusines and murexias drawn from cytochrome-*b*, 12S-rRNA, protamine-P1 genes. The same criticism of invalid outgroup choice could apply, however, to their use of *Phascogale*. A morphology-based phylogeny of similar topology to Armstrong et al. (1998) is produced using taxa from Table 8 and employing *Phascogale* as the outgroup. The New Guinea clade (*M. rothschildi*, *M. longicaudata*, *A. naso*, *A. melanurus*, *A. habbema*) however, is defined by one synapomorphy (Character 58) and 9 reversals (Characters 27, 29, 30, 37, 50, 60, 71, 72, 73), with 1 homoplasious reversals and 3 homoplasious forwards step. (The node underpinning Australian and New Guinean taxa is defined by 1 synapomorphy (Character 5), 14 reversals (Characters 2, 3, 6, 8, 10, 11, 15, 32, 33, 39, 40, 52, 57, 69) and 4 homoplasious reversals.

If the fossil record and outgroup comparisons can be trusted to correctly polarise characters for the dasyurid ancestor, rooting the tree on a derived member of the dasyuridae can reverse polarity of the tree, forcing plesiomorphic taxa into clades based on their most derived members with subsequent branches being occupied by progressively more primitive taxa. Then, of course the nodes are defined by reversals.

Subsequent genetic studies, however, using non-dasyurid outgroups (*Myrmecobius*, Krajewski et al., 1993; *Peroryctes*, Kirsch et al., 1990; *Homo*, *Mus*, *Ornithorhynchus*, Krajewski

formerly Western Australian Museum, Paul Horner, Northern Territory Museum and Art Gallery and John Woinarski, Conservation Commission of the Northern Territory.

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LITERATURE CITED

- APLIN, K.P., BAVERSTOCK, P.R. & DONNELLAN, S.C. 1993. Albumin immunological evidence for the time and mode of origin of the New Guinea terrestrial mammal fauna. *Science in New Guinea* 19(3): 131-145.
- ARCHBOLD, R., RAND, A.L. & BRASS, L.J. 1942. Results of the Archbold Expeditions. No.41. Summary of the 1938-1939 New Guinea Expedition. *Bulletin of the American Museum of Natural History* 79: 199-288.
- ARCHER, M. 1976a. Miocene marsupicarnivores (Marsupialia) from central South Australia, *Ankotarinja tirarensis* gen. et sp. nov., *Keeuna woodburni* gen. et sp. nov., and their significance in terms of early radiations. *Transactions of the Royal Society of South Australia* 100: 53-73.
- 1976b. The dasyurid dentition and its relationships to that of didelphids, thylacinids, borhaenids (Marsupicarnivora) and peramelids (Peramelina: Marsupialia). *Australian Journal of Zoology Supplementary Series* No. 39: 1-34.
- 1976c. Revision of the marsupial genus *Planigale* Troughton (Dasyuridae). *Memoirs of the Queensland Museum* 17: 341-465.
- 1976d. The basicranial region of marsupicarnivores (Marsupialia), inter-relationships of carnivorous marsupials, and affinities of the insectivorous marsupial peramelids. *Journal of the Linnean Society of London* 59: 217-322.
1981. Results of the Archbold Expeditions. No. 104. Systematic revision of the marsupial dasyurid genus *Sminthopsis* Thomas. *Bulletin of the American Museum of Natural History* 168: 61-224.
- 1982a. Review of the dasyurid (Marsupial) fossil record, integration of data bearing on phylogenetic interpretation, and suprageneric classification. Pp. 397-443. In Archer, M. (ed) *Carnivorous marsupials Vol. 2.* (Royal Zoological Society of New South Wales: Sydney).
- 1982b. A review of Miocene thylacinids (Thylacinidae, Marsupialia), the phylogenetic position of the Thylacinidae and the problem of apriorisms in character analysis. Pp. 445-476. In Archer, M. (ed) *Carnivorous marsupials Vol. 2.* (Royal Zoological Society of New South Wales: Sydney).
- ARMSTRONG, L.A., KRAJEWSKI, C. & WESTERMAN, M. 1998. Phylogeny of the dasyurid marsupial genus *Antechinus* based on cytochrome-b, 12S-rRNA, and protamine-P1 genes. *Journal of Mammalogy* 79(4): 1379-1389.
- BARBOUR, R.A. 1977. Anatomy of marsupials. Pp. 237-272. In Stonehouse, B. and Gilmore, D. (eds) *The biology of marsupials.* (The Macmillan Press Ltd: London).
- BAVERSTOCK, P.R., ARCHER, M., ADAMS, M. & RICHARDSON, B.J. 1982. Genetic relationships among 32 species of Australian dasyurid marsupials. Pp. 641-650. In Archer, M. (ed.) *Carnivorous marsupials Vol. 2.* (Royal Zoological Society of New South Wales: Sydney).
- BAVERSTOCK, P.R., KRIEG, M. & BIRRELL, J. 1990. Evolutionary relationships of Australian marsupials as assessed by albumin immunology. *Australian Journal of Zoology* 37: 273-287.
- BONAPARTE, C.L. 1838. *Synopsis vertebratorum systematis.* *Nuoviannali delle Scienze Naturali Bologna* 2: 105-133.
- BRAITHWAITE, R.W. 1973. An ecological study of *Antechinus stuartii* (Marsupialia: Dasyuridae). Unpubl. MSc thesis, University of Queensland.
- BRASS, L.J. 1959. Results of the Archbold Expeditions. No. 79. Summary of the fifth Archbold expedition to New Guinea. *Bulletin of the American Museum of Natural History* 118: 1-69.
1964. Results of the Archbold Expeditions. No. 86. Summary of the sixth Archbold Expedition to New Guinea (1959). *Bulletin of the American Museum of Natural History* 127: 145-216.
- BREMER, K. 1990. Combinable component consensus. *Cladistics* 6: 369-372.
- CORBET, G.B. & HILL, J.E. 1980. A world list of mammalian species. (British Museum (Natural History) & Comstock: London).
- DOLLMAN, G. 1930. On the mammals obtained by Mr. Shaw Mayer in New Guinea, and presented to the British museum by Mr. J. Spedan Lewis F.R.Z. *Proceedings of Zoological Society of London*: 429-435.
- DWYER, P. 1977. Notes on *Antechinus* and *Cercartetus* (Marsupialia) in the New Guinea Highlands.

TABLE 7. Character states (defined in derived state) used to resolve affinities of *Murexia* and *Antechinus*.

- UPPER INCISORS: 1. Incisor row transverse. 0 = V or U-shaped; 1 = transverse.
 2. Incisors procumbent. 0 = not procumbent; 1 = slightly procumbent; 2 = more than 1; 3 = procumbent.
 3. I¹ crown relatively bulky with cingulum low. 0 = crown of I1 a thin spur; 1 = more bulky than 0; 2 = bulkier than 1; 3 = bulkier than 2; 4 = bulkier than 3; 5 = bulkier than 4; 6 = crown heavy.
 4. I¹ laterally compressed, elongate. 0 = I¹ needle or peg-like; 1 = more compressed than 0; 2 = more compressed than 1; 3 = paddle-like.
 5. R and L I¹ separated by wide diastema. 0 = touching; 1 = narrowly spaced; 2 = widely spaced.
 6. I¹ non-needle-like. 0 = I¹ needle-like; 1 = less needle-like than 0; 2 = less needle-like than 1; 3 = less needle-like than 2; 4 = less needle-like than 3; 5 = less needle-like than 4; 6 = spatulate or club-shaped.
 7. I¹ and I² juxtaposed. 0 = I¹ and I² widely spaced; 1 = spacing less than 0; 2 = spacing less than 1; 3 = spacing less than 2; 4 = spacing less than 3; 5 = crushed.
 8. I²⁻⁴ crowns broader than roots. 0 = crown-root width equal; 1 = crown slightly broader; 2 = broader than 1; 3 = broader than 2; 4 = broader than 3; 5 = crown much broader than root.
 9. I²⁻⁴ lensate, elongate. 0 = I²⁻⁴ peg-like; 1 = more elongate than 0; 2 = more than 1; 3 = more than 2; 4 = lensate.
 10. I²⁻⁴ crowns broad (occlusal) and cusps folded lingually. 0 = crowns narrow and cusps unfolded; 1 = crowns broader and slightly folded; 2 = more than 1; 3 = more than 2; 4 = crowns broad and folded.
 11. I² > I³ > I⁴. 0 = I⁴ > I³ > I²; 1 = I⁴ - I³ - I²; 2 = I² > I³ > I⁴; 3 = I² > I³ > I⁴; 4 = I² > I³ > I⁴.
 12. I¹⁻⁴ cingulated. 0 = no cingulation; 1 = slight cingulation; 2 = more than 1; 3 = more than 2; 4 = heavily cingulated.
 13. I⁴ with posterior cusp. 0 = No posterior cusp; 1 = posterior cusp present.
 14. Total upper incisors = 8. 0 = 10; 1 = 8.
 15. I² greatly enlarged. 0 = no; 1 = yes.
 UPPER CANINES: 16. C¹ relatively short. 0 = very long; 1 = shorter than 0; 2 = shorter than 1; 3 = short.
 17. C¹ root and crown clearly differentiated. 0 = no differentiation; 1 = differentiated; 2 = more than 1; 3 = more than 2.
 18. C¹ bulky, non needle-like. 0 = needle-like; 1 = less than 0; 2 = less than 1; 3 = less than 2; 4 = cone-shaped.
 19. C¹ non-caniniform. 0 = caniniform; 1 = less than 0; 2 = premolariform.
 20. C¹ with posterior cusp. 0 = cusp absent; 1 = small cusp present.
 UPPER PREMOLARS: 21. P¹ circular in occlusal view. 0 = elongate; 1 = More rounded than 0; 2 = more rounded than 1; 3 = more rounded than 2.
 22. P¹ and P² touching or crushed. 0 = wide space between P¹ and P²; 1 = small space between P¹ and P²; 2 = P¹ and P² touch or crushed.
 23. P¹ and P² with postero-lingual lobing. 0 = no lobing; 1 = slight lobing; 2 = pronounced lobing; 3 = very pronounced lobing.
 24. P³ with large posterior cusp. 0 = no cusp; 1 = slight cusp; 2 = pronounced cusp.
 25. P³ greatly reduced or lost. 0 = no; 1 = yes.
 UPPER MOLARS: 26. M¹⁻³ narrow with incomplete anterior cingulum. 0 = M¹⁻³ broad, cingulum complete; 1 = narrow, cingulum incomplete or nearly so; 2 = narrow, cingulum incomplete, molars very narrow.
 27. M¹ anterior margin (protocone to stylar cusp A) indented or concave. 0 = convex or straight; 1 = indented or concave.
 28. M² shorter than M³. 0 = no, M² > M³; 1 = yes.
 29. M²⁻⁴ protocone width greatly reduced. 0 = protocone broad; 1 = protocone narrower than 0; 2 = narrower than 1; 3 = narrower than 2.
 30. M¹ stylar cusp B greatly reduced. 0 = no reduction, almost coplanar with D; 1 = reduced; 2 = greatly reduced.
 31. M⁴ protocone reduced. 0 = protocone large; 1 = protocone slightly reduced; 2 = reduction greater than 1; 3 = reduction greater than 2; 4 = reduction greater than 3; 5 = reduction greater than 4; 6 = reduction greater than 5; 7 = reduction greater than 6.
 32. M⁴ preparacrista orients obliquely to longitudinal axis of skull. 0 = orientation transverse to longitudinal; 1 = slightly oblique; 2 = oblique.
 33. M¹, M² stylar cusp D greatly enlarged. 0 = stylar cusp D a low crest; 1 = taller than 0; 2 = taller than 1; 3 = stylar cusp D tall and conical.
 34. M², M³ ectoloph greatly indented. 0 = no; 1 = slight indent; 2 = more than 1; 3 = greatly indented.
 35. M⁴ metacone loss. 0 = metacone small; 1 = metacone more reduced than 0; 2 = more than 1; 3 = more than 2; 4 = metacone lost.
 36. M^x posterior cingulum absent. 0 = present; 1 = absent.
 37. M¹ paracone and stylar cusp B fused. 0 = no, widely separated; 1 = approximated; 2 = greater approximation than 1; 3 = fused.

TABLE 7 (Cont.).

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- LOWER INCISORS: **38.** I_1, I_2 prostrate. $0 = I_1, I_2$ almost perpendicular to dentary axis. $1 =$ more prostrate than 0 ; $2 =$ almost horizontal.
- 39.** I_3 heel narrower than heel of I_1 . $0 = I_3$ heel wider than heel of I_1 heel; $1 =$ heels equal width; $2 = I_3$ heel slightly narrower; $3 =$ narrower than 2 ; $4 =$ narrower than 3 .
- LOWER PREMOLARS: **40.** $P_3 < P_2$. $0 = P_3 > P_2$; $1 = P_3 \leq P_2$; $2 = P_3 < P_2$.
- 41.** Lower premolars crushed. $0 =$ premolars widely spaced; $1 =$ nearly touching; $2 =$ slightly crushed; $3 =$ more than 2 ; $4 =$ more than 3 .
- 42.** P_1, P_2 in contact. $0 =$ widely spaced; $1 =$ just contacting; $2 =$ crushed.
- 43.** P_3 broad or oriented transversely. $0 = P_3$ longitudinal with dentary axis; $1 =$ broad; $2 =$ transverse to dentary axis.
- 44.** P_{1-3} almost circular in occlusal view. $0 =$ premolars elongate; $1 =$ premolars oval; $2 =$ premolars almost round.
- 45.** P_2 , or P_3 lenticular. $0 =$ not lenticular; $1 =$ very narrow; $2 =$ lenticular.
- 46.** P_3 cingulated. $0 =$ not cingulated (or P_3 absent); $1 =$ cingulated.
- 47.** P_1, P_2 with postero-lingual lobing. $0 =$ no lobing; $1 =$ slight lobing; $2 =$ heavily lobed.
- 48.** P_3 single-rooted or absent. $0 =$ neither; $1 =$ yes, single-rooted or absent.
- LOWER MOLARS: **49.** M_1 paraconid reduced. $0 =$ paraconid well developed; $1 =$ paraconid more reduced than 0 ; $2 =$ paraconid more reduced than 1 .
- 50.** M_3 talonid much narrower than trigonid. $0 =$ no; $1 =$ yes.
- 51.** M_4 talonid with reduced cusp. $0 = 3$ cusps, well developed; $1 = 3$ cusps, poorly developed; $2 = 2$ cusps; $3 = 1$ cusp; $4 =$ loss of talonid.
- 52.** M_2 entoconid reduced. $0 =$ entoconid tall; $1 =$ reduced; $2 =$ greatly reduced; $3 =$ absent.
- 53.** M_1 paraconid absent. $0 =$ present; $1 =$ absent.
- 54.** M_{1-3} metacristids and hypocristids not transverse to long axis of dentary. $0 =$ transverse; $1 =$ not transverse.
- CRANIAL FEATURES: **55.** Skull brachycephalic (ratio skull width between lachrymal canals to length I_1 -lachrymal canal). $0 =$ elongate (67-75%); $1 =$ less elongate than 0 (76-84%); $2 =$ less elongate than 1 (85-93%); $3 =$ less elongate than 2 (94-102%); $4 =$ skull brachycephalic (103-111%).
- 56.** Nasals non-fluted. $0 =$ fluted; $1 =$ less fluted than 0 ; $2 =$ less fluted than 1 ; $3 =$ flat.
- 57.** Tympanic wing of the alisphenoid greatly expanded. $0 =$ tympanic wing small; $1 =$ tympanic wing greatly expanded.
- 58.** Expansion of the pars mastoidea and adjacent squamosal. $0 =$ no expansion; $1 =$ expansion.
- 59.** Nasals expanded posteriorly. $0 =$ not expanded; $1 =$ expanded.
- 60.** Skull flat, not domed. $0 =$ domed; $1 =$ less than 0 ; $2 =$ flat or concave; $3 =$ dorso-ventrally flattened.
- 61.** Squamosal-frontal contact. $0 =$ no; $1 =$ yes.
- 62.** Palatine vacuities. $0 =$ not present; $1 =$ present.
- EXTERNAL FEATURES: **63.** Supratragus folded. $0 =$ simple; $1 =$ folded.
- 64.** Tail very short or very long. $0 =$ slightly shorter than head-body; $1 =$ much shorter or much longer than head-body.
- 65.** Hind foot pads highly developed and striated post-metatarsal pads present. $0 =$ no; $1 =$ yes; $2 =$ well developed.
- 66.** Claws very long. $0 =$ no; $1 =$ yes.
- 67.** Body with longitudinal stripe. $0 =$ no; $1 =$ yes.
- 68.** Backward-opening pouch. $0 =$ no, rudimentary; $1 =$ pouch; $2 =$ yes, backward-opening.
- 69.** Tail with terminal brush. $0 =$ no; $1 =$ yes.
- 70.** Body size large. $0 =$ very small; $1 =$ larger than 0 ; $2 =$ larger than 1 ; $3 =$ large.
- 71.** Penile morphology complex. $0 =$ simple, non-bifid glans; $1 =$ small bifurcation of glans; $2 =$ deeply cleft and divided penis; $3 =$ acquisition of accessory corpora cavernosa or penis appendage.
- 72.** Males die soon after mating. $0 =$ no; $1 =$ yes.
- 73.** Nipple number high and variable. $0 = 4$; $1 = 6$; $2 = 8$; $3 = 10$; $4 = 12$; $5 =$ variable.
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- KIRSCH, J.A.W., KRAJEWSKI, C., SPRINGER, M.S. & ARCHER, M. 1990. DNA/DNA hybridization studies of carnivorous marsupials. II. Relationships among dasyurids (Marsupialia: Dasyuridae). *Australian Journal of Zoology* 38: 673-696.
- KLUGE, A.G. & FARRIS, J.S. 1969. Quantitative phyletics and the evolution of anurans. *Systematic Zoology* 38: 7-25.
- KRAJEWSKI, C., PAINTER, J., DRISCOLL, A.C., BUCKLEY, L. & WESTERMAN, M. 1993. Molecular systematics of New Guinea dasyurids (Marsupialia: Dasyuridae). *Science in New Guinea* 19: 157-166.
- KRAJEWSKI, C., PAINTER, J., BUCKLEY, L. & WESTERMAN, M. 1994. Phylogenetic structure of the marsupial family Dasyuridae. *Journal of Mammalian Evolution* 2: 25-35.
- KRAJEWSKI, C., BUCKLEY, L., WOOLLEY, P.A. & WESTERMAN, M. 1996. Phylogenetic analysis of cytochrome b sequences in the dasyurid subfamily Phascogalinae: systematics and evolution of reproductive strategy. *Journal of Mammalian Evolution* 3(1): 81-91.
- KRAJEWSKI, C., BUCKLEY, L. & WESTERMAN, M. 1997. DNA phylogeny of the marsupial wolf resolved. *Proceedings of the Royal Society of London B* 264: 911-917.
- LAURIE, E.M.O. 1952. Mammals collected by Mr Shaw Mayer in New Guinea 1932-1949. *Bulletin of the British Museum (Natural History)*, London 1: 271-318.
- LAURIE, E.M.O. & HILL, J.E. 1954. List of land mammals of New Guinea, Celebes and adjacent islands 1758-1952 (British Museum (Natural History): London).
- LEE, A.K., WOOLLEY, P.A. & BRAITHWAITE, R.W. 1982. Life history strategies of dasyurid marsupials. Pp. 1-11. In Archer, M. (ed.) *Carnivorous marsupials Vol. 1*. (Royal Zoological Society of New South Wales: Sydney).
- LEE, A. K & COCKBURN, A. 1985. *Evolutionary ecology of marsupials*. (Cambridge University Press: London).
- LUCKETT, W.P. 1993. An ontogenetic assessment of dental homologies in therian mammals. Pp. 182-284. In Szalay, F.S. & McKenna, M.C. (eds) *Mammal phylogeny*. (Springer-Verlag: New York).
- MANN, G.F. 1958. Reproduccion de *Dromiciops australis* (Marsupialia: Didelphidae). *Investigaciones Zoológicas Chilaenas* 4: 209-213.
- MARSHALL, L.G. 1977. Cladistic analysis of the borhyaenoid, dasyuroid, and thylacinid (Marsupialia: Mammalia) affinity. *Systematic Zoology* 26: 410-425.
1982. Systematics of the South American family Microbiotheriidae. *Fieldiana: Geology*, n.s. 10: 1-75.
- MENZIES, J.I. 1972. The relative abundance of *Planigale novaeguineae* and other small mammals in the south Papuan savannas. *Mammalia* 36: 400-405.
- MUIRHEAD, J. 1994. Systematics, evolution and palaeobiology of recent and fossil bandicoots (Marsupialia: Paramelomorphia) from Miocene deposits of Riversleigh, northwestern Queensland. Unpubl. PhD thesis, University of New South Wales.
- MUIRHEAD, J. & ARCHER, M. 1990. *Nimbacinus dicksoni*, a Plesiomorphic thylacine (Marsupialia: Thylacinidae) from Tertiary deposits of Queensland and the Northern Territory. *Memoirs of the Queensland Museum* 28(1): 203-221.
- NIXON, K.C. 1992. *Clados*, Version 1.2. Program and documentation (Trumansburg: New York).
- NIXON, K.C. & CARPENTER, J.M. 1993. On outgroups. *Cladistics* 9: 413-426.
- REIG, O.A., KIRSCH, J.A.W. & MARSHALL, L. 1987. Systematic relationships of the living and neocenozoic American opossum-like marsupials (Suborder Didelphimorphia), with comments on the classification of these and of the Cretaceous and Palaeogene New World and European metatherians. Pp. 1-89. In Archer, M. (ed.) *Possums and opossums, studies in evolution*. Vol. 1 (Surrey Beatty & Sons Pty Ltd and The Royal Zoological Society of New South Wales: Sydney).
- RETIEF, J.D., KRAJEWSKI, C., WESTERMAN, M. & DIXON, G.H. 1995. The evolution of Protamine P1 genes in dasyurid marsupials. *Journal of Molecular Evolution* 41: 549-555.
- RIDE, W.D.L. 1964. A review of Australian fossil marsupials. *Journal and Proceedings of the Royal Society of Western Australia* 47: 97-131.
- RIDGWAY, R. 1912. *Color Standards and Color Nomenclature*. (Ridgway: Washington).
- SCHLEGEL, H. 1866. *Phascogale longicaudata*. *Nederlandse Tijdschrift voor de Dierkunde* 3: 356-357.
- SEGALL, W. 1969. The middle ear region of *Dromiciops*. *Acta Anatomica* 72: 489-501.
- SIMPSON, G.G. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History*: 85.
- STEIN, G.H.W. 1932. Einige neue beuteltiere aus Neu-guinea. *Zeitschrift für Säugetierkunde* 7: 256-257.
- SWOFFORD, D.L. 1999. *PAUP*. Phylogenetic Analysis Using Parsimony (and other Methods). Version 4. (Sinauer Associates: Sunderland, Massachusetts).
- TATE, G.H.H. 1938. New or little-known marsupials: a new species of Phascogalinae, with notes upon *Acrobates pulchellus* Rothschild. *Novitates Zoologicae* 41: 58-60.
1947. Results of the Archbold Expeditions. No. 56. On the anatomy and classification of the Dasyuridae (Marsupialia). *Bulletin of the American Museum of Natural History* 88: 101-155.
- TATE, G.H.H. & ARCHBOLD, R. 1936. Results of the Archbold Expeditions. No. 8. Four apparently new polyprotodont marsupials from New Guinea. *American Museum Novitates* 823: 1-4.

1937. Results of the Archbold Expeditions. No. 16. Some marsupials of New Guinea and Celebes. Bulletin of the American Museum of Natural History 73: 331-476.
1941. Results of the Archbold Expeditions. No. 31. New rodents and marsupials from New Guinea. American Museum Novitates 1101: 1-9.
- THOMAS, M.O. 1888. Catalogue of Marsupialia and Monotremata in the collection of the British Museum (Natural History). (British Museum: London).
1899. Description of a new *Phascogale* from British New Guinea, obtained by Dr. L. Loria. Annali del Museo Civico di Storia Naturale Giacomo Doria, Genova 20 (ser.2): 191-192.
- 1903a. On a collection of mammals from the small islands off the coast of Western Panama. Novitates Zoologicae 10: 39-42.
- 1903b. On a small collection of mammals from the Rio de Oro, Western Sahara. Novitates Zoologicae 10: 300-302.
1904. Exhibition of specimens and descriptions of new species of mammals from New Guinea. Annals and Magazine of Natural History 14: 402.
1912. Notes on *Phascogale* and *Chaetocercus*. Annals and Magazine of Natural History 9: 91-92.
1913. Expedition to the Central Western Sahara by Ernst Hartert. Mammals. Novitates Zoologicae 20: 28-33.
- THOMAS, M.O. & MARTIN, A.C. 1920. Captain Angus Buchanan's air expedition. 1. On a series of small mammals from Kano. Novitates Zoologicae 17: 315-320.
- van der FEEN, P.J. 1962. Catalogue of the marsupials of New Guinea, the Moluccas and Celebes in the Museo Civico Di Storia Naturale 'Giacomo Doria' in Genoa. Annali del Museo Civico di Storia Naturale Giacomo Doria, Genova 73: 19-70.
- VAN DYCK, S. 1980. The Cinnamon Antechinus, *Antechinus leo* (Marsupialia: Dasyuridae), a new species from the vine-forests of Cape York Peninsula. Australian Mammalogy 3: 5-17.
- 1982a. The status and relationships of the Atherton Antechinus, *Antechinus godmani* (Marsupialia: Dasyuridae). Australian Mammalogy 5: 195-210.
1988. Phylogenetics of Papua New Guinean and Irian Jayan dasyurids. Bulletin of the Australian Mammal Society, (Abstract: 23).
- WESTERMAN, M. & WOOLLEY, P.A. 1993. Chromosomes and the evolution of dasyurid marsupials: an overview. Science in New Guinea 19(3): 123-130.
- WOOLLEY, P.A. 1984. Phallic morphology of the New Guinean species of *Antechinus*. Bulletin of the Australian Mammal Society 8: 182 (Abstract).
1987. Phallic morphology of *Dasyuroides byrnei* and *Dasyurus cristicauda* (Marsupialia: Dasyuridae). Australian Journal of Zoology 35: 535-540.
1989. Nest location by spool-and-line tracking of dasyurid marsupials in New Guinea. Journal of Zoology, London 218: 689-700.
1994. The dasyurid marsupials of New Guinea: use of museum specimens to assess seasonality of breeding. Science in New Guinea 20 (1): 49-55.
- WOOLLEY, P.A. & WEBB, S.J. 1977. The penis of dasyurid marsupials. Pp. 307-323. In Stonehouse, B. & Gilmore, D. (eds) The biology of marsupials. (The Macmillan Press Ltd: London).
- WROE, S. 1999. The geologically oldest dasyurid, from the Miocene of Riversleigh, north-west Queensland. Palaeontology 42 (3): 501-527.
- ZIEGLER, A.C. 1977. Evolution of New Guinea's marsupial fauna in response to a forested environment. Pp. 117-138. In Stonehouse, B. & Gilmore, D. (eds) The biology of marsupials. (The Macmillan Press Ltd: London).
1982. An ecological check-list of New Guinea Recent mammals. Pp. 863-894. In Gressitt, J.L. (ed.) Biogeography and ecology of New Guinea. (Junk: The Hague).

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